Links between lateral riparian vegetation zones and flow

Michiel Karl Reinecke

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Supervisors: Professors Karen Esler, Cate Brown and Jackie King

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DECLARATION

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This dissertation includes 5 original unpublished publications. The development and writing of the papers were the principle responsibility of myself and, for each of the cases where this is not the case, a declaration is included in the dissertation indicating the nature and extent of the contributions of co-authors.

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ABSTRACT

Riparian vegetation communities that occur along perennial rivers are structured in lateral zones that run parallel to river flow. This dissertation investigated the structure of South African riparian vegetation communities along perennial, single-thread headwater streams. The central assumption was that lateral zones result from differential species' responses to changing abiotic factors along a lateral gradient up the river bank. It was first necessary to establish the pattern of zones and whether this pattern occurs repetitively and predictably on different rivers in different biomes. Since the flow regime is considered to be the master variable that controls the occurrence of lateral zones, the link between flow as the major abiotic driver and the distribution of plants in zones was determined. Predictions were made with respect to how variable flow may influence phenological traits, particularly with respect to seed dispersal, and physiological tolerances to drying out and were tested.

The existence of lateral zones at reference sites in the Western Cape of South Africa was explored and their vegetation characteristics were described. Plant distribution was related to bank slope, as defined by elevation and distance from the wetted channel edge during summer (dry season) low flow, indicating a direct link to river bank hydraulics. Whether or not the same zonation patterns occur in riparian communities in other parts of South Africa was explored next. The four zones described for Fynbos Riparian Vegetation were evident at all of the other rivers tested, despite major differences in geographic location, vegetation community type, climate and patterns of seasonal flow. The four lateral zones could be separated from each other using a combination of flood recurrence and inundation duration. Functional differences were investigated between three tree species that occur in Fynbos Riparian Vegetation. Functional differences were apparent with respect to timing of seed dispersal, growth in branch length versus girth and three physiological measures of tolerance to drying out; specific leaf area ($cm^2.g^{-1}$), wood density ($g.cm^{-3}$) and levels of carbon isotopes ($\delta^{13}C$). In order to determine the impact of invasive alien plants and to monitor recovery after clearing, the physical rules devised to help delineate zones were used to locate lateral zones that had been obliterated after invasion and subsequent clearing. At the sites invaded by *A. mearnsii* plants, the zone delineations showed that invasion started in the lower dynamic zone, where adult and sapling *A. mearnsii* were most abundant. In un-invaded systems, this zone was the least densely vegetated of the four zones, the most varied in terms of inundation duration and the frequency of inter- and intra-annual floods, and was an area of active recruitment comprised mainly of recruiting seedlings and saplings.

An understanding of the functional differences between lateral zones was a common thread at each riparian community that was linked to the annual frequency of inundation and the period, when inundated.

OPSOMMING

Oewer plantegroei gemeenskappe wat langs standhoudende riviere voorkom is gestruktureer in laterale sones parallel met die rivier vloei. Hierdie verhandeling ondersoek die struktuur van Suid-Afrikaanse oewer plantegroei gemeenskappe langs standhoudende, enkelloop hoof strome. Die sentrale aanname was dat laterale sones vorm as gevolg van verskillende spesies se reaksie teenoor die verandering van abiotiese faktore teen 'n laterale gradiënt met die rivierbank op. Dit was eers nodig om die patroon van die gebiede vas te stel en uit te vind of hierdie patroon herhaaldelik en voorspelbaar binne verskillende riviere in verskillende biome voorkom. Aangesien die vloeiwyse beskou word as die hoof veranderlike wat die teenwoordigheid van laterale sones beheer, is die skakel tussen die vloei, as die belangrikste abiotiese bestuurder, en die verspreiding van plante in sones bepaal. Voorspellings is gemaak met betrekking tot hoe veranderlike vloei fenologiese eienskappe kan beïnvloed, veral met betrekking tot die saad verspreiding, en fisiologiese toleransie teen uitdroog, en is getoets.

Die bestaan van laterale sones binne verwysings studie terreine in die Wes-Kaap van Suid-Afrika is ondersoek en hul plantegroei eienskappe is beskryf. Plant verspreiding was verwant aan bank helling, soos gedefinieer deur hoogte en afstand vanaf die nat kanaal rand gedurende somer (droë seisoen) lae vloei, en dui dus op 'n direkte skakel met die rivier bank hidroulika. Of dieselfde sonering patrone voorkom in oewer gemeenskappe in ander dele van Suid-Afrika is volgende verken. Die vier sones beskryf vir fynbos oewer plantegroei was duidelik by al die ander riviere wat ondersoek is, ten spyte van groot verskille in geografiese ligging, plantegroei gemeenskap tipe, klimaat en patrone van seisoenale vloei. Die vier laterale sones kan onderskei word van mekaar deur middel van 'n kombinasie van vloed herhaling en oorstroomde toestand duur. Funksionele verskille is ondersoek tussen drie boom spesies wat voorkom in Fynbos Oewer Plantegroei. Funksionele verskille was duidelik met betrekking tot tydsberekening van saad verspreiding, groei in tak lengte tenoor omtrek, en drie fisiologiese maatstawwe van verdraagsaamheid teenoor uitdroging; spesifieke blaar area ($cm^2.g^{-1}$), hout digtheid ($g.cm^{-3}$) en vlakke van koolstof isotope ($\delta^{13}C$). Ten einde die impak van indringerplante te bepaal en die herstel na ontbossing te monitor is die fisiese reëls voorheen vasgestel om sones te help baken gebruik om laterale sones, wat vernietig is na indringing en die daaropvolgende ontbossing, te vind. Op die terreine wat deur *A. mearnsii* indringerplante binnegeval is, het die indeling van sones getoon dat die indringing begin het in die laer dinamiese sone, waar volwasse en klein *A. mearnsii* bome die volopste was. In stelsels wat nie binnegeval is deur indringerplante was hierdie sone die minste dig begroei van die vier sones, die mees verskillend in terme van oorstroomde toestand duur en die frekwensie van inter-en intra-jaarlikse vloede, en was 'n gebied van aktiewe werwing hoofsaaklik bestaande uit rekruut saailinge en boompies.

'n Begrip van die funksionele verskille tussen laterale sones was 'n algemene verskynsel by elke oewer gemeenskap wat gekoppel was aan die jaarlikse frekwensie van oorstroming en die oorstroomde toestand duur.

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1 Introduction

Riparian vegetation communities occur along rivers in lateral zones parallel to the direction of river flow. Similar patterns of lateral zonation appear to occur along rivers across the world despite variability in flow regime, topographical setting and climate. The flow regime is considered to be the master variable responsible for the occurrence of these lateral zones as it directs, *inter alia*, river channel structure, moisture regimes and the life histories of the plants that grow there (Naiman *et al.* 2005).

This dissertation seeks to quantify the links between river flow and lateral vegetation zones in riparian areas. Understanding, and if possible quantifying, these links aids prediction of how riparian communities would change in response to altered flow regimes. River flow regimes may change in response to water-resource development and/or water abstraction or as part of rehabilitation projects.

Riparian vegetation plays a central role in river ecosystem functioning: bank erosion is lessened through reductions in flow velocity at the wetted edge and through increased bank stability via root buttressing (Thorne 1990); water quality is maintained through trapping of sediments, nutrients and other organic matter (Lozovik *et al.* 2007), and shading regulates water temperature and primary productivity (Vannote *et al.* 1980); food is provided for riparian animals in the form of fruits, nuts and leaves, and for aquatic macroinvertebrates in the form of leaf litter (King 1981); and the plants themselves offer a diverse array of habitats as well as a corridor for the movement of migratory terrestrial and semi-aquatic animals and plant propagules (Prosser 1999; Terrill 1999). Riparian vegetation also acts as a moderator of water flow and sediment transport by intercepting precipitation and runoff, increasing infiltration and channel roughness (Thorne 1990), which slows flow and moderates bank erosion (Coops *et al.* 1996); reducing soil moisture and water levels in alluvial aquifers and river flow through evapotranspiration (Viddon and Hill 2004); effecting changes to soil nutrient cycles by leaf litter inputs (Dwire 2001); and altering channel structure through inputs of large woody debris (Ward *et al.* 2002). The nature and extent of the riparian vegetation is intimately linked to river channel structure and water availability (Naiman *et al.* 2005) and so in many ways, this important component of the river ecosystem is vulnerable to change through human activities within the catchment.

This dissertation deals with the influence of surface (river) water availability[1], but it is acknowledged that groundwater, interflow and soil moisture also contribute significantly to water availability in the riparian area. Sediments and surface flow interact and influence the kinds of plants suited to a particular channel shape and prevailing water regime (Poole 2002). Consequently, changes in the flow regime will elicit a response in the nature and extent of the riparian vegetation (Poff *et al.* 1997). This response, and its knock-on effects on other aspects of the riverine ecosystem, is fundamental knowledge needed in the science of Environmental Flows, as is an understanding of the reason behind the distribution patterns of riparian plants along different rivers.

1.1 Definitions

1.1.1 Riparian area

In this dissertation, the word riparian area refers to that portion of river bank directly influenced by the presence of a perennially flowing river (Naiman *et al.* 2005). Riparian areas are ecotones (Swanson *et al.* 1992) that occupy a three-dimensional (Wilson and Imhoff 1998) transitional area between aquatic and terrestrial ecosystems. They serve as conduits for the exchange of materials and energy between the two ecosystems (Richardson

[1] In this dissertation, unless otherwise indicated, further use of the term water availability refers to surface (river) flow.

et al. 2007) and generally exhibit sharp gradients in environmental and ecological processes (Swanson *et al.* 1992; Naiman *et al.* 1998). Typically, riparian vegetation communities occur as a mosaic of patches associated with different soil types and moisture regimes (Naiman and Decamps 1997) and thus show considerable variation in species richness and composition (Corbacho *et al.* 2003).

1.1.2 Riparian vegetation

In this dissertation riparian vegetation refers to the riverine plant community sustained by generally moist conditions along river margins. The riparian vegetation of perennial rivers can be defined as the vegetation community that is supported by the area of land adjacent to the wetted channel of a permanently flowing river, and that is distinctly different in species composition from neighbouring terrestrial communities. The lower boundary of the study area at a site was the dry-season wetted channel edge, and so aquatic plants were excluded.

1.1.3 Environmental Flows

The term Environmental Flows (see Section 2.3.2), as used here, is defined as the water that is left in a river system, or released into it, for the specific purpose of managing the ecological condition of that river (Brown and King 2006).

1.1.4 Lateral vegetation zones

The term *lateral zone* is used for sub-sections of the riparian area from the dry-season wetted channel edge to the outer boundary of the riparian zone, in which groups of plants preferentially grow in association with one another based on their shared habitat requirements and adaptations to withstand prevailing hydrogeomorphological conditions.

1.2 Focus of the dissertation

This dissertation focuses on the riparian vegetation of perennial rivers in South Africa and excludes riparian zones[2] of lakes, wetlands and floodplains. Rivers (lotic systems) and lakes/wetlands (lentic systems) operate under different hydrogeomorphological[3] controls and thus support a different biota and have different ecological functioning. Lakes and wetlands experience less dynamic and more diffuse flow than rivers and are thus generally lower-energy environments subjected to lower levels of disturbance (Innis *et al.* 2000). Rivers, by comparison, are higher-energy ecosystems associated with flow in well-defined channels that are shaped by system resetting disturbances (Rountree *et al.* 2008). Two main characteristics separate riverine riparian areas from other riverine ecosystems (Rogers 1995): (1) a linear form dictated by their connection with rivers and (2) a hydrological connection to upstream and downstream areas. To my knowledge, there are no comparative studies of zonation patterns between riparian communities situated in different biomes. There are multiple linked controls on, and drivers of, riparian vegetation population dynamics, such as floods, drought, fire, anthropogenic disturbances, multiple paths for available water and that riverine ecosystems are multi-dimensional, patchy landscapes (Naiman *et al.* 2005). However, the conceptual framework (Section 2.4) was focussed on surface (river) flow of headwater streams (Gomi *et al.* 2002) and floodplains were avoided in order to minimise vertical and lateral linkages that characterise floodplains. Only perennial rivers were selected, seasonal/ephemeral ones where groundwater plays a larger role in riparian life

[2] Please note that the terms riparian zone and riparian area were used interchangeably to reduce the incidence of the word zone in this dissertation, as there are also lateral and longitudinal zones.
[3] Hydrogeomorphological: the interaction of hydrologic processes with landforms and/or the interaction of geomorphic processes with surface and subsurface water (Sidle and Onda 2004).

histories were avoided. Recently burnt riparian areas were also avoided, other than where this was incorporated as a disturbance factor.

In southern Africa riparian vegetation community structure has been correlated with, *inter alia*:

- indirect gradients, such as elevation, distance from channel and substratum type (van Coller 1992; van Coller *et al.* 1997, 2000; Reinecke *et al.* 2007);
- direct gradients such as flood frequency, stream power and depth to ground water (Hughes 1988, 1990; Boucher 2002); and
- resource gradients, such as water availability, soil moisture and nutrient status (Birkhead *et al.* 1997; Botha 2001).

However, since these are interrelated, it is likely that one or more key abiotic variables could be used to understand the structure and arrangement of riparian vegetation. Once these are established for different kinds of rivers and/or flow regimes in one area, then they could inform Environmental Flow studies on similar rivers where there is a dearth of information on the riparian vegetation, the flow regime or the relationship between the two.

The central assumption (Figure 1.1) is that lateral riparian vegetation zones along rivers result from differential species' responses to a combination of abiotic factors that vary in space and time (van Coller 1992). In order to develop a framework that describes lateral zones in riparian plant communities, a mechanistic explanation for characteristic differences between the lateral zones must be established. To achieve this it is first necessary to establish the pattern of zones and to test whether this pattern occurs repetitively and predictably on different rivers in one biome. If the same pattern occurs on different rivers it would suggest that similar zones will be present on rivers in other biomes. If the same pattern is demonstrated despite differences in season flow regimes, climate and species present, it would suggest the same abiotic factors may be responsible. Since the flow regime is considered to be the master variable that controls the occurrence of lateral zones, links between flow as the major abiotic driver and the distribution of plants in zones must be tested. Flow is considered to influence riparian communities in three main ways (van Coller 1992): as an agent of disturbance (floods); as a resource necessary for growth and reproduction; and as a stressor during periods of prolonged low flow. The incidence of flooding and the period of inundation experienced during a flood are expected to be important abiotic factors that may limit plant distribution due to differences in physiological tolerances and variable abilities of the plants to withstand the force of floods. It is also expected that the timing of floods may be linked to plant phenology, particularly seed set, and the incidence of floods may be linked to physiological tolerances to variation in water availability. Establishing functional differences between characteristic species of the zones would contribute to a mechanistic explanation for the occurrence of lateral zones.

Accordingly, key questions are posed in each subsequent Chapter:

- Chapter 2 - Literature review.
- Chapter 3 – Lateral zones in Fynbos Riparian Vegetation.
- Chapter 4 – Links between lateral vegetation zones and river flow.
- Chapter 5 – Functional differences between lateral zones in Fynbos Riparian Vegetation.
- Chapter 6 – Using a reference condition of lateral zones to assess recovery of Fynbos Riparian Vegetation.

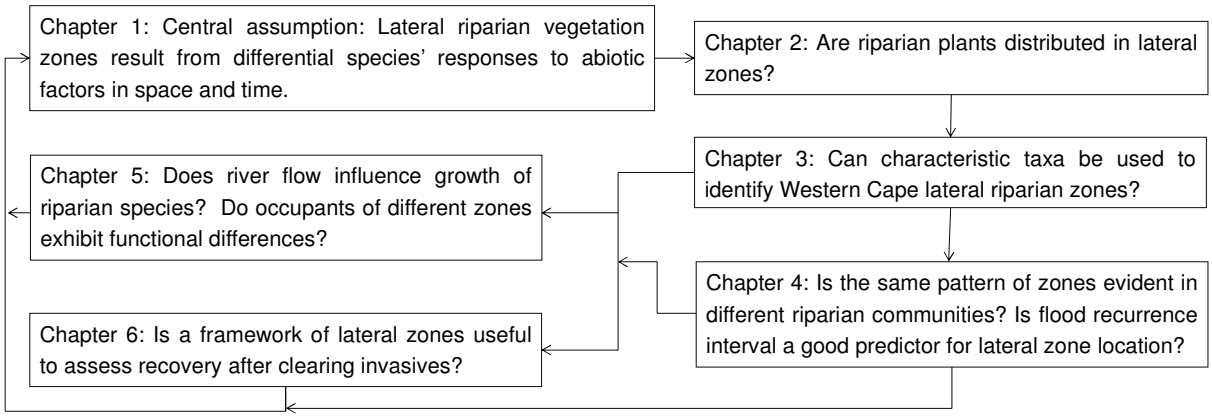

Figure 1.1 Key questions in five chapters.

The focus of the literature review was to summarise evidence for the occurrence of lateral vegetation zones and the understanding of abiotic controls said to influence such zones in order to establish a conceptual framework (Chapter 2). The key questions emanating from Chapter 2 led to hypotheses that were tested in the four data Chapters (3 – 6).

The existence of lateral riparian zones at reference sites in the Western Cape of South Africa was explored in Chapter 3 in order to test whether the arrangement of plants in zones was repetitive and predictable on different rivers, and secondly whether characteristic plant taxa are restricted to specific zones. A description of the vegetative characteristics of the lateral zones was provided along with physical rules that used river channel shape to help delineate the zones.

Chapter 4 explored the pattern of zones in other riparian communities situated in different parts of South Africa with different climates and markedly different hydrographs. Three hypotheses were tested that related to whether the same pattern is repeated in different biomes regardless of species composition, and if so, whether the same abiotic flow variables, being the incidence of floods and the period of inundation when flooded, related equally well to the distribution of zones.

Chapter 5 explored how seasonal flow may influence plant phenology, particularly seed dispersal. Two predications detailing expected differences between species that occupy different lateral zones; i.e. that seeds are dispersed preferentially into the zone in which the species occurs most frequently and secondly that a protracted period of flowering should take place since floods occur unpredictably. Similarly, functional differences were expected between plants that occupy different zones and predictions made with respect to plant growth and physiological tolerance to drying out.

Chapter 6 explored an application of the rules that were developed in Chapter 3 in order to locate lateral zones that had been obliterated at invaded and cleared sites in order to test whether new insight may be revealed regarding the process of invasion. The first hypothesis tested river basin-scale relationships between invaded, cleared and reference sites, while the second related to the process of invasion and whether zones differed in their susceptibility to invasion, based on the differences in species composition between zones (Chapter 3) and the variability in inundation duration and frequency of flooding experienced (Chapter 5).

The final Chapter 7 synthesises the conclusions of the four data sections, Chapters 3 – 6. As per University requirements, Chapters 2 – 6 were written as papers but have been streamlined to reduce repetition in the dissertation. To this end, the abstracts were removed, the introductions of the data Chapters 3 – 6 were shortened, and the methods of data collection and analysis were cross-referenced between chapters where applicable.

2 Literature review

Karen Esler, Cate Brown and Jackie King are co-authors as each contributed towards the concepts therein and reviewed the manuscript.

This review targeted literature that reports on links between patterns of riparian vegetation zonation and flow. The key question was, "Are riparian plant species distributed in lateral zones?" (Figure 1.1). Focus was directed towards data that quantify the hypothesized relationships and concepts that argue reasons for the occurrence of lateral riparian zones. Synthesis was sought on naming conventions and methods to discern hydrogeomorphological controls on riparian plant distribution in riverine ecosystems. Throughout the dissertation, comparisons were drawn between larger floodplain rivers of the northern hemisphere and the smaller South African headwater streams that were my subject, since such southern African rivers differ considerably from those in the northern hemisphere where many of the studies of riparian ecology have taken place. The conceptual framework was developed around these differences, primarily the hydrogeomorphological differences between floodplain rivers and headwater streams. Also, since most principles of riparian vegetation recruitment dynamics have been based upon the ecology of large floodplain rivers (Mahoney and Rood 1998; Rood *et al.* 1999), hypotheses were developed to test the relevance of these theories to the life histories of riparian species in headwater streams, given the obvious differences in flow pattern and channel structure.

2.1 Flow and the structure of river channels

The physical structure of a river ecosystem and its associated habitats is determined by the size of the river channel; its position in the drainage basin; the underlying geology and geomorphological setting; the hydrological (flow) regime; and the regional climate (Naiman *et al.* 2005). At a local level, however, the composition and structure of riparian communities are influenced primarily by river channel shape and surface flow (Naiman *et al.* 2008). These are represented by the inter-related disciplines of hydrology and fluvial geomorphology, often combined into the field of hydrogeomorphology.

River morphology (width, depth and planform) is adjusted by the flow of water and sediment supplied from the drainage basin (Newson and Newson 2000). As river gradient decreases downstream, so does the capacity of the river to transport sediment. As this occurs, sediments of ever smaller calibre are deposited on the river bed (Church 2002). Thus, mountain streams consist of large calibre sediments, such as boulders and cobbles, whereas lowland rivers usually have beds comprised of fine sediments, such as gravel, sand and mud (Rowntree *et al.* 2000). Although changes in channel structure occur on a continuum from source to mouth, various authors have described geomorphological zones characterised by differences in sediment transport and deposition (Rowntree *et al.* 2000). These basin-scale concepts are discussed below followed by a summary of geomorphological classification of South African rivers that includes physical descriptors at a finer scale.

2.1.1 Basin scale concepts of river channel structure

A river basin comprises three transfer zones: a production zone in the headwater streams where erosion and transport of sediment are higher than deposition; a transfer zone where sediment transport and deposition are in equilibrium; and a deposition zone at the lower end of the system (Schumm 1977). Montgomery (1999) introduced the concept of Process Domains, which he defined as river-basin components that differ in sediment supply and transport. According to Schumm (1977), hill slopes are the primary source of sediment supplied to river channels in the headwater streams and are sediment-supply limited. He described river channels as links between headwater streams and lowlands where sediments are re-cycled through processes of erosion and deposition. In the Process Domain concept, floodplains store sediment for long cycles between floods but act as a source of sediment

during large flood events. Church (2002) and Ward *et al.* (2002) developed these concepts further by describing river systems as a series of alternating laterally constrained channels and laterally expansive floodplains, driven by changes in flow, sediment supply and sediment transport. These concepts are useful when considering how the structure of riparian zones might change along the river between Process Domains.

Both Church (2002) and Ward *et al.* (2002), distinguish rivers with floodplains from those with narrow, constrained river channels. In their descriptions, river channels and floodplains increase in width and complexity down the rivers' length as the balance between sediment supply and transport shifts from supply-limited channels upstream to transport-limited channels downstream. This occurs as more sediment becomes available lower down the river, driving changes in channel structure from straight to meandering, and then to braided and anastomosing. Straight channels have a sinuous thalweg[4] and may comprise alternating lateral bars of a variety of sediments that move slowly downstream. Meandering channels comprise a single-thread channel with alternating eroding (concave) and aggrading (convex) channel banks that migrate downstream. Multi-channel rivers are either:

- braided rivers of multiple shifting channels that are highly mobile with unvegetated, unconsolidated gravel and sand bars, or stable and vegetated mid-channel bars, or
- anastomosing rivers with large permanently vegetated islands.

Channels in the upper reaches of river basins (headwater streams) are laterally constrained by v-shaped channels and so have limited capacity to store sediment and other organic matter. The dominant direction in which matter and biota are transported is longitudinally downstream. Since there is limited floodplain development, river flow acts directly on the hill slopes (said to be coupled; Church 2002), the riparian zone is often narrow, and the influence of groundwater and the presence of alluvial aquifers is limited (Groeneveld and Griepentrog 1985). Further downstream, floodplain valleys and meandering lowland rivers receive sediment from headwater streams and are less coupled to hill-slope sediment sources. Although a river may alternate between single channel and floodplain reaches at any point along its length, floodplain development usually increases with distance downstream and results in a greater complexity of vertical (between the river and its bed) and lateral interactions (between the river and its floodplain). As floodplains increase in extent and frequency, the influence of, and exchange between, the river and its subterranean counterpart, the alluvial aquifer also increases (Ward and Stanford 1995). The ecotone between surface water and alluvial groundwater, known as the hyporheic zone, may extend for kilometres away from the river beneath a floodplain (Boulton *et al.* 2010). These longitudinal, vertical and lateral exchanges of matter and biota are important aspects of the functioning of floodplain systems (Ward *et al.* 2002) when contextualising research studies. In this dissertation, abiotic/biotic links between riparian vegetation and the surface flow of headwater streams, that are easier to model hydraulically as flow moves predominantly in a longitudinal direction, were tested. The influence of groundwater and soil moisture, for example, were not considered in the development of the conceptual framework despite their importance for river ecosystem functioning, since flow alone presented sufficient scope.

2.1.2 A hierarchical geomorphological classification for South African rivers

Geomorphologists describe drainage basins as multi-scaled, nested hierarchies where the basic building blocks of landscape elements are grouped beneath larger elements, which are controlled and operate over successively longer time frames and larger spatial scales. Rowntree *et al.* (2000) delineate South African rivers into longitudinal zones, dividing channel features further into segments, reaches, morphological units and biotopes (Table 2.1).

[4] The lowest elevation of surface flow within the active channel.

Table 2.1 The zonal classification system for South African rivers (Rowntree *et al.* 2000).

Longitudinal zone	Range of slope	River characteristics
Source zone	Not specified	Low gradient, headwater plateau or headwater basin able to store water. Spongy or peaty hydromorphic soils.
Mountain headwater stream	>0.1	A very steep gradient river dominated by vertical flow over bedrock with waterfalls and plunge pools. Normally first or second order. Reach types include bedrock fall and cascades.
Mountain stream	0.04-0.099	Steep gradient river dominated by bedrock and boulders, locally cobble or coarse gravels in pools. Reach types include cascades, bedrock fall, step-pool. Approximate equal distribution of 'vertical' and 'horizontal' flow components.
Transitional	0.02-0.039	Moderately steep river dominated by bedrock or boulder. Reach types include plane-bed, pool-rapid or pool-riffle. Confined or semi-confined valley floor with limited flood plain development.
Upper foothills	0.005-0.0019	Moderately steep, cobble-bed or mixed bedrock-cobble bed channel, with plane-bed, pool-riffle, or pool-rapid reach types. Length of pools and riffles/rapids similar. Narrow flood plain or sand, gravel or cobble often present.
Lower foothills	0.001-0.005	Lower gradient mixed bed alluvial channel with sand and gravel dominating the bed, locally may be bedrock controlled. Reach types include pool-riffle or pool rapid, sand bars common in pools. Pools of significantly greater extent than rapids or riffles. Flood plain often present.
Lowland river	0.0001-0.0009	Low gradient alluvial fine bed channel, typically regime reach type. May be confined, but fully developed meandering pattern within a distinct flood plain develops in unconfined reaches where there is an increased silt content in bed or banks.
Additional zones associated with a rejuvenated longitudinal profile		
Rejuvenated bedrock fall/cascades	>0.02	Moderate to steep gradient, often confined channel (gorge) resulting from uplift in the middle to lower reaches of the long profile, limited lateral development of alluvial features, reach types include bedrock fall, cascades and pool-rapid.
Rejuvenated foothills	0.001-0.0019	Steepened section within middle reaches of the river caused by uplift, often within or downstream of gorge; characteristics similar to foothills (gravel/cobble bed rivers with pool-riffle/ pool-rapid morphology) but of a higher order. A compound channel is often present with an active channel contained within a macro-channel activated only during infrequent flood events. A flood plain may be present between the active and macro-channel.
Headwater flood plain	>0.005	A headwater low gradient channel often associated with uplifted plateau areas as occur beneath the eastern escarpment.

Longitudinal zones are areas within the basin that are considered to be uniform with respect to flood runoff and sediment production and are the units that freshwater ecologists most frequently use to describe differences along the continuum of change down a river, for example mountain streams versus foothills. Within zones, segments are channel lengths over which no significant change in discharge or sediment load occurs. There should be an overall similarity in channel type within a segment particularly with respect to valley form, channel dimensions and sediment calibre. Each segment comprises a number of different reaches, with each kind of reach sharing local constraints on channel form, a characteristic channel pattern (straight or sinuous) and degree of incision. Reaches are comprised of morphological units that may be either hydraulic controls (such as rapids or riffles) or pools that tend to occur in alternating sequences. Morphological units are the basic building blocks considered by geomorphologists. Within this classification, the river channel is defined as either alluvial or bedrock controlled, and morphological units are either erosional (pools) or depositional (hydraulic controls, such as riffles or rapids). For example, a mountain stream ZONE may contain a narrow valley and a bedrock controlled SEGMENT, which consists of a series of rapid-pool REACHES characterised by alternating rapid and pool MORPHOLOGICAL UNITS. This hierarchy may be used to select study sites with comparable prevailing hydrogeomorphological conditions, at the spatial scale of interest, between river basins.

2.1.3 Riparian areas as ecological landscapes

Running water erodes bedrock and terrace soils, and redistributes alluvium (Standford 1998). Thus, the pattern and variety of water flows ultimately determine the landscape. At the scale of these morphological units, certain landscape elements turnover at a high rate as pools are scoured and/or lateral bars formed. Wu and Loucks (1995) proposed the Hierarchical Patch Dynamics paradigm based on the assumption that geomorphic processes vary spatially and temporally across a basin and that biotic systems respond dynamically to this. The paradigm combines four major limnological concepts that shift in importance at different positions in the river basin. The River Continuum (Vannote *et al.* 1980) and the Serial Discontinuity (Ward and Stanford 1983) concepts, which explain upstream-downstream linkages while the Flood-Pulse (Junk *et al.* 1989), and the Hyporheic Corridor (Stanford and Ward 1993) concepts, which explain lateral and vertical interactions between the river channel, the floodplain and groundwater. The Hierarchical Patch Dynamics paradigm encompasses the idea that riverine ecosystems are structured according to the degree to which connectivity is shared between different landscape elements. Along the continuum from source to mouth, and hill slopes to lowland floodplains, riparian substrata continually and alternately build up, lie fallow, gradually deconstruct or erode (Naiman *et al.* 2005). For example, if the physical structure of a river limits lateral and vertical connectivity, as occurs in bedrock controlled systems, the riverine communities are under the control of upstream-downstream processes, as described by the River Continuum Concept and Serial Discontinuity Concept. If on the other hand, a river's structure emphasizes lateral or vertical connectivity, such as in floodplain systems, riverine communities are more likely under the control of lateral and vertical processes, as described by the Flood-Pulse Concept and the Hyporheic Corridor Concept. Together, these incorporate interactions between spatial patterns and ecological processes in a way that is relevant to river channels and riparian zones (Naiman *et al.* 2005), and as such it emphasizes the unique nature of each lotic ecosystem's patch hierarchy and a non-linear functioning of community dynamics (Poole 2002).

2.2 Variable flow regimes and the consequences for riparian vegetation

River flow has a direct influence on riverine biota (Naiman *et al.* 2005). Key principles to contextualise these abiotic/biotic links are encapsulated in the Natural Flow Regime paradigm (Poff *et al.* 1997). These principles may be translated to South African rivers once we understand how South African river flow compares to rivers elsewhere in the world.

2.2.1 The Natural Flow Regime paradigm

The guiding principle of the Natural Flow Regime paradigm is that the integrity of lotic (flowing) ecosystems depends largely upon their natural dynamic character (Poff *et al.* 1997). The natural flow regime varies from time scales of hours and days to seasons over years and longer, and flow is considered the 'master variable' that dictates the abundance and distribution of riverine species (Resh *et al.* 1998). Components of the flow regime are described in terms of magnitude, frequency, duration, timing and rate of change of flow. These characterise the range of river flows from floods to low flows, each of which is critical for different species in some way (Poff *et al.* 1997, adapted using King *et al.* in press):

- Flow magnitude or discharge, which is the amount of water moving past a fixed point per unit time.
- Flow frequency of occurrence, which describes how often a flow of a certain magnitude recurs over a specified time interval. For example, a 100-year flood is equalled or exceeded on average once every 100 years and so has a 0.01 chance of occurring in any one year.
- The average (median) flow, which is determined from a data series over a specific time interval and has a frequency of occurrence of 0.5, i.e., 50%.
- Flow duration is the period over which a flow event is experienced.

- Flow timing, or predictability of a flow event, which refers to the regularity with which an event or a given magnitude occurs. For example, annual peak flows may occur with low or high seasonal predictability.
- The rate of change or flashiness, which refers to the speed at which the flow increases or decreases. So-called 'flashy rivers' (Gordon *et al.* 1992) have rapid rates of change in the quantity of water flowing down them but overall variability is also important as it indicates how flows may become muted.
- Onsets of flow seasons and duration of flow during wet and dry seasons, which refers to the average Julian day, in a hydrological year, when flow-season change: flood season, transition 1 (flood recession), dry season and transition 2 (flood onset).

Surface flow in rivers ultimately derives from precipitation but, at any given time, may comprise a combination of surface runoff, soil water and groundwater (Viddon and Hill 2004). Climate, geology, topography, soils and vegetation all play a role in water supply and the path that flow may take (Gurnell 1997). Variability in intensity, timing and duration of precipitation combined with the effects of soil texture, topography and plant evapotranspiration contribute to locally- and regionally-variable flow patterns (Poff and Ward 1989). Thus, generalisations about hydrological properties, between headwater streams and lowland rivers for example, should be made with caution since natural flow characteristics are highly variable across river basins in response to properties such as climate, geology and topography (Naiman *et al.* 2008). For instance, Baker and Wiley (2009) found different valley types can present similar hydrological conditions and thus elicit similar responses even from different riparian vegetation communities. They describe how prolonged seasonal variation can occur in small basins with brief lag times and high water tables as well as in larger basins with attenuated lag time and low groundwater yields. They also demonstrate that similar basins may manifest different hydrological conditions through different combinations of valley shape or other topographical or localised factors.

2.2.2 River flow in South Africa

The flow regimes of southern African rivers differ from those of rivers in temperate climates where many of the studies of riparian ecology have taken place. The coefficient of variation[5] in mean annual runoff, the variability in flooding (measured as the standard deviation of the logarithms of the annual peak discharge) and the extreme floods index (measured as the ratio between the 100-yr flood and the mean annual flood) are all higher for southern African rivers than for Australia, the South Pacific, Asia, South America, North America and Europe (Walling 1996). Australian and southern African flow regimes are most similar, while those on other continents tend to have much lower values. Similarly, the average inter-annual variability of runoff (Coefficient of variation [CV] = 1.13) is much higher for South African rivers (Görgens and Hughes 1982) than for rivers in Australia (CV = 0.7) and the rest of the world (0.25 < CV < 0.4; Lloret *et al.* 2006). The conversions of mean annual precipitation (MAP) into mean annual runoff (MAR) are extremely low in South Africa and Australia compared to other countries. In South Africa, the MAP:MAR is 8.6% and in Australia it is 9.8%, while Canada by comparison has a conversion of 65.7% (Dollar and Rowntree 2003). Also, many of the studies of riparian vegetation recruitment dynamics are from large floodplain rivers (Mahoney and Rood 1998; Rood *et al.* 1999), whereas in South Africa only very few of the rivers are associated with extensive floodplains (Davies *et al.* 1995).

The rainfall:runoff ratio (MAP:MAR) varies considerably across South Africa in response to climate, vegetation, geology, slope and when the basin was last saturated (Joubert and Hurley 1994). Much of the country experiences summer rainfall and a dry winter. The Western Cape with its Mediterranean climate, i.e., winter rainfall and a dry summer, is the exception, although rainfall in the mesic southern coastal region is aseasonal (Joubert and

[5] CV is measured as the ratio of the standard deviation and the mean. A high CV may be indicative of high disturbance and low predictability (Gordon *et al.* 1992).

Hurly 1994). Almost all the rivers in South Africa exhibit a 'flashy' runoff response that is considered to be fairly typical of arid or semi-arid countries (Gordon *et al.* 1992). Flood events have short lag times relative to rainfall events in the basin, and steep ascending and receding limbs. Although the wet and dry seasons occur with some regularity, the frequency and magnitude of floods in the wet season are considered to be unpredictable (Ractliffe 2009). Flow variability is ecologically important as the life histories of riverine biota are thought to evolve in response to various levels of flow variability/predictability (Resh *et al.* 1998). There are few detailed studies of flow-linked recruitment dynamics and/or community succession in South Africa it is expected that their biotic communities should be dominated by hardy opportunists (Winterbourn *et al.* 1981, cited by Davies *et al.* 1995), with generalist regeneration requirements (Gooderham and Barmuta 2007), since generalist traits are expected in species that inhabit heterogeneous environments (Devictor *et al.* 2008).

2.2.3 Categorising rivers in South Africa

Joubert and Hurly (1994) classify river flow across South Africa using two different sets of flow variables:

- seasonal patterns of flow;
- flow type characteristics, such as:
    - temporal predictability and variability; and
    - flood characteristics, for example the number of floods per year, the median number of day intervals between floods, the median duration of floods, flood predictability, and the median day of the year on which floods occurred.

They describe seven seasonal groups:

- two geographically distinct groups: the winter peak flow region of the south-western Cape and the aseasonal/early spring region of the southern and eastern Cape;
- four groups in the summer rainfall region not divided into clear geographic regions;
    - moderate summer peak flow (December to February) between KwaZulu Natal and Mpumalanga;
    - midsummer extreme peak flow (January and February) throughout Mpumalanga and the Orange Free State;
    - midsummer moderate peak flow (February) inland of the coastal belt and mixed with others in Mpumalanga; and
    - moderate late summer peak flow (February and March) in coastal Transkei and Natal.
- One group with extreme spring peak flow in November in the Eastern Cape.

They recognise three main groups of rivers that differ in terms of flow-type characteristics:

- A group with mainly extreme-seasonal but also episodic flow and a high degree of constancy[6] (zero flow in this instance) located in the interior.
- A mixture of groups recording extreme-seasonal, semi-perennial and perennial flow separated into two main groups in terms of the interval between floods:
    - Those with a short interval between floods, thus a medium to high flood frequency and with floods of long duration (10 days compared to all the other groups with 3 days). These rivers have a high degree of constancy and are located in Mpumalanga and KwaZulu Natal. Another group in this category of short interval between floods consists of rivers scattered throughout the country (with the exception of the Transkei and KwaZulu Natal coastal belts) where overall predictability[7] is the lowest of any group, flood durations are shorter and constancy is medium to low.

[6] Constancy is the part of predictability that describes flows that remain similar throughout a hydrological year (Colwell 1974).

[7] Predictability is defined in two parts: constancy and contingency, with contingency being that part of predictability that describes the regularity of seasonal flow events (Colwell 1974).

  - Those with a long interval between floods with low overall predictability and low flood frequency and found along the southern and eastern Cape coastal belt. Another group in this category of long intervals between floods consists of rivers with very low constancy and flood frequency but with the highest degree of seasonal predictability of all the groups. These are found mainly in the south-western Cape.
- A perennial super group:
  - Rivers with medium to low flood durations (1-6 days) characterised by high degree of constancy and medium predictability. There is one sub-group with short intervals between floods and thus a high flood frequency, found mainly to the east of the escarpment and in the south-western Cape. Another sub-group is the largest grouping of perennial rivers, with medium to long intervals between floods, very low flood frequencies and high flood predictability with rivers located mainly to the east of the escarpment and in the south-western Cape. A final sub-group of rivers with slightly lower flood duration but extremely long intervals between floods and thus very low flood frequencies.

In general, the patterns of perennial flow along the subtropical coast and the plateau slopes of the Transkei, KwaZulu Natal and Mpumalanga are similar, with moderate midsummer and moderate late summer peaks, while flow type is perennial (Joubert and Hurly 1994). The southern and Eastern Cape coastal belt are clearly distinct and characterised by aseasonal flow or a slight early spring peak; a flow regime not commonly found elsewhere in the country. Overall predictability is very low, with a fairly high flood frequency and the lowest flood predictability of all groups. The Western Cape is characterised by winter peak flow with low overall predictability and high seasonal predictability. Sites were selected in these three broadly different areas for the national comparison of lateral zones and their links to the flow regime (Chapter 4).

2.3 Flow and the response of riparian vegetation

Riparian vegetation communities are dynamic and the relative dominance of species changes from river source to river mouth. Areas of broadly similar physical habitat contain broadly similar communities, but the species composition and density at any one site is affected by changes in soil moisture, nutrient status and topography (Van Coller 1992); the frequency and intensity of droughts and floods, fire, plant disease and grazing, biogeographical distributions (Naiman *et al.* 2005); and species interactions (Francis 2006).

Localised maintenance of populations and persistence depends upon site stability, site suitability for germination and establishment, and favourable ambient environmental conditions until the age of reproduction (Hupp and Osterkamp 1996). Successful recruitment depends upon (1) availability of seed or propagules, (2) colonisable habitat, (3) a recruitment window where moisture favours establishment and (4) resilience to high (floods) and low (drought) flow periods (Tabacchi *et al.* 1998). Sufficient flows are required seasonally to recharge ground water levels at the end of the dry season and also to facilitate vegetation recruitment (dispersal, germination and seedling growth), which usually occurs as floods recede. Some specialist riparian species release seed to coincide with flood recession because moist seedbeds become available for colonisation (Naiman *et al.* 2008). Plants cued to release seed in this way are reproductive specialists that require specific conditions in order for recruitment to be successful. These reproductive specialists are the most sensitive to alterations in the flow regime, and may be subject to recruitment failure if the flow regime is altered. Scouring floods clear new areas for recruitment and newly established seedlings expand their roots to maintain contact with the gradually receding water table (Rood *et al.* 1999). Other riparian plants may be less specific in their response, flowering and setting seed over many months of the year, or in response to periods of high flow only. These generalists are often pioneers and the first species to colonise new habitat (alluvial

deposits), as their seedlings are able to germinate under a variety of hydrogeomorphological conditions and are less prone to recruitment failure as a result of changes to the flow regime.

The life histories of northern temperate floodplain specialists are intimately linked with the annual flood peak (Mahoney and Rood 1998). For instance, seed release of *Populus* and *Salix* in the northern temperate forests is linked to a range of water levels that present optimal positions for seedling dispersal to germination sites. The hydrochorous (water-dispersed) seeds preferentially germinate on new sandy alluvial deposits, termed nursery sites. For successful seeding establishment to occur, the rate of the surface/groundwater recession should be slow enough to allow seedling root extension to keep pace with the drop in water level, thereby avoiding moisture stress. Evidence suggests that pioneering soft-wood species such as these are tolerant of fluvial action, burial and submersion, but are vulnerable to shade and drought (Mahoney and Rood 1998). Once passed the seedling stage, water availability may be the dominant factor controlling survival. The Recruitment-box Model (Mahoney and Rood 1998; Rood *et al.* 1999) describes the flow-linked life histories of *Populus* and *Salix* and assumes that river stage and alluvial groundwater decline are closely coupled. The relatively clear-cut relationships between inundation levels and plant life-histories in this model, is the reason that attempts to reverse the negative impacts of development-linked flow changes on the riparian vegetation of these rivers focus on reinstating the timing (and magnitude) of the natural flow regime.

In southern Africa, four studies describe community structure and population dynamics of floodplain forests in the north of the country and in Kenya (Hughes, 1988, 1990; van Coller 1992; van Coller *et al.* 1997, 2000; Mackenzie 1999; and Botha 2001). Three others address community composition and structure along Western Cape rivers (Sieben 2003; Galatowitsch and Richardson 2005; Vosse *et al.* 2008). Hughes (1988) and van Coller (1992) present empirical evidence for links between lateral zones and indirect gradients, such as elevation and distance from the wetted channel along the Tana River floodplain in Kenya and the Sabie River in the Kruger National Park respectively. They both describe flood recurrence and water availability, either as soil moisture or precipitation, to be important factors influencing community structure. Hughes (1990) links her community types with flood recurrence intervals, while van Coller *et al.* (1997, 2000) links his with geomorphic channel features and those of the floodplain. Mackenzie *et al.* (1999) and Botha (2001) both investigate recruitment dynamics of Lowveld Riverine Forest (see Mucina and Rutherford 2006 for a community description) by incorporating the combined influences of hydrology, geomorphology (sediment calibre), rainfall, fecundity, survival probabilities, density dependence and population structure. Their hypotheses link changes in community structure to flood events and geomorphic changes in river channel structure and sediment calibre. These studies describe seral[8] succession of floodplain communities in lateral zones; much like the studies of northern temperate floodplain forests. None link flow components to exact floodplain positions (elevation and distance vectors from wetted channel edge) due to a combination of the complexity of the floodplain geomorphic mosaic and inaccurate/incomplete hydrological data.

Sieben (2002) delineates lateral zones in Fynbos Riparian Vegetation (Mucina and Rutherford 2006) communities of Western Cape headwater streams but could not link these to flow, again due to inaccurate hydrological data. Galatowitsch and Richardson (2005) present evidence suggesting that disturbance-driven seedling recruitment, as for riparian plants in floodplain forests, may not be an adaptive advantage for riparian trees of headwater streams. They suggest that seedlings germinate preferentially on stable banks and rock fractures rather than on recent alluvial deposits, while Vosse *et al.* (2008) reveal that seeds of Fynbos Riparian trees are absent from the riparian seed bank. They conclude that the riparian vegetation of Western Cape headwater streams is dominated by re-sprouters, and

[8] Seral succession is the development towards a climax community by the establishment and growth of similarly sized individuals that increase in age laterally up the bank (Barbour and Dwight 2000).

not by re-seeders as postulated although the dependence of alternately reproducing sexually versus asexually in this community has not been described.

This circumstantial evidence suggests that headwater streams may function differently to larger rivers with floodplains. Certainly, the links between the life histories of South African riparian plants and the flow regime require further investigation (see Chapter 4). To facilitate this, it is necessary to develop a conceptual framework for controls on the distribution of lateral zones across a riparian area, which requires a classification of lateral zones. Lateral zones are the subject of Chapter 3.

2.3.1 Lateral zone characterisation

Riparian zones are divided into a number of lateral zones distinguished by the composition and abundance of species, and characterised by links with flow (Bendix 1999; Taman 2001; Boucher 2002; Lite *et al.* 2005; Thayer *et al.* 2005; Dwire *et al.* 2006; and Baker and Wiley 2009) and landforms (Harris 1988; Moon *et al.* 1997; Vadas *et al.* 1997; Bendix and Hupp 2000; Godfery 2000; van Coller 1992; van Coller *et al.* 1997, 2000; Rountree *et al.* 2008; and Sieben and Reinecke 2008).

The first comprehensive categorisation of lateral riparian zones for southern Africa was by Boucher and Tlale (1999) for the Senqu River in Lesotho. Seven lateral zones were proposed related to decreasing flood-recurrence intervals up the bank. This was later formalised using data from the Breede River (Western Cape, South Africa) into three main groups (Boucher 2002):

- the aquatic zone divided into the:
    - permanent aquatic sub-zone, inundated 95% of the year;
    - rooted aquatic sub-zone, inundated 50% of the year;
- the wet bank zone divided into:
    - the sedge or moss sub-zone, wetted by the Class 1 floods[9];
    - the shrub or *Prionium* sub-zone, wetted by the Class 2 and 3 floods;
- the dry bank zone divided into:
    - the lower dynamic sub-zone, wetted by the Class 4 floods;
    - the tree-shrub sub-zone wetted, by the 1:2 to the 1:20 year floods; and
    - the back dynamic sub-zone wetted, by the 1:20 to 1:100 year floods.

Reinecke *et al.* (2007) found evidence of four lateral zones at or above the dry-season water level along reference-condition rivers in the Western Cape: a wet edge adjacent to the wetted channel; a channel fringe next up the bank; a transitional zone between the wet edge and the tree-shrub zone; the tree-shrub zone, and an outer transitional zone, situated between the tree-shrub zone and the adjacent terrestrial community. Using canopy-cover data irrespective of rooted position, they identified links between lateral zonation and distance and elevation from the wetted edge of the channel, but could not show links to the flow regime, as canopy cover was insufficiently accurate for modelling plant position. Thus, links between flood-recurrence intervals and lateral zones remain a hypothesis that needs to be tested and is the subject of Chapter 4. The most recent categorisation of lateral zones in South Africa is that of the Riparian Vegetation Response Assessment Index (VEGRAI, Kleynhans *et al.* 2007), which is used to assess the present-day condition of riparian vegetation relative to a hypothetical reference condition by taking historical impacts into consideration. Assessments are made for three lateral zones that are loosely correlated to periods of inundation. The marginal zone is inundated intra-annually, the lower zone with a recurrence of 1-3 years, and an upper zone at intervals >3 years. The position of the zones is determined by their proximity to the wetted channel, bank topography and the presence of terrestrial species.

[9] Flood-classes 1-4 are all intra-annual floods (Brown *et al.* 2006). Class 1 floods = dry season base flow; Class 2 floods = wet season base flow; Class 3 floods = wet season freshes; Class 4 floods = half the size (in volume) of the 1:2 year flood.

The three categorisations compare quite well (Table 2.2) despite the fact that the data collection and analytical methods differ substantially. The cohesion between the descriptions provides some support for the notion that characteristic features of the lateral zones can be linked to flow patterns. They also illustrate the use of different terms for the same bank position. Only Boucher (2002) includes the aquatic zone in his classification of lateral zones. The other studies describe one lateral zone at the wetted edge, and Boucher separates this into two zones. Both Boucher (2002) and Reinecke *et al.* (2007) describe transitions between the wet and dry bank (the lower dynamic and channel fringe respectively), and between the tree-shrub and the terrestrial zones (the back dynamic and outer transitional respectively). Kleynhans *et al.* (2007) does not distinguish transitional zones but describes the upper zone as being transitional between riparian and terrestrial vegetation.

Table 2.2 A comparison of lateral zonation descriptions for South African riparian vegetation. (T = a transitional zone). (Adapted from Reinecke *et al.* 2007).

<table>
<tr><th>Bank position</th><th>Boucher (2002)</th><th>Reinecke et al. (2007)</th><th>Kleynhans et al. (2007)</th></tr>
<tr><td rowspan="2">Aquatic</td><td>Permanent</td><td>Not addressed</td><td>Not addressed</td></tr>
<tr><td>Rooted aquatic macrophytes</td><td rowspan="2">Wet edge</td><td rowspan="2">Marginal</td></tr>
<tr><td rowspan="3">Wet bank</td><td>Fringing sedge</td></tr>
<tr><td>Shrub willow</td><td rowspan="2">Channel fringe (T)</td><td rowspan="2">Not addressed</td></tr>
<tr><td rowspan="2">Dry bank</td><td>Lower dynamic (T)</td></tr>
<tr><td>Tree-shrub</td><td>Tree-shrub</td><td>Lower</td></tr>
<tr><td rowspan="2">Terrestrial</td><td rowspan="2">Back dynamic (T)</td><td rowspan="2">Outer transitional (T)</td><td rowspan="2">Upper (T)</td></tr>
</table>

Boucher's (2002) transition from wet to dry bank is located at the 1:2 year flood recurrence interval, which concurs with the change from Kleynhans *et al.'s* (2007) marginal to the lower zone, located between the 1- and 3-year flood recurrence interval. The occurrence of lateral zones in riparian vegetation communities should link to characteristic landforms such as terraces, or mid-channel bars, and it may be no coincidence that these align with the channel forming discharge return period of 1 to 2 years (Gordon *et al.* 1992), although Dollar and Rowntree (2003) found no compelling evidence that flow events with a return period of 1 to 2 years are responsible for maintaining channel form in South African rivers. They propose that a range of low flows are responsible for transporting the bulk of bed material and for morphological adjustment of the wetted channel; a larger 'reset' discharge, with an average recurrence of 20 years, maintains the macro-channel and mobilises the entire bed. In this regard, it is interesting that Boucher's (2002) transition between the outer dry bank communities, the tree-shrub and the back dynamic, is located at the 1:20 year recurrence interval.

In this dissertation, the naming convention of Kleynhans *et al.* (2007) is adopted as a starting point because it is the one most frequently used by South African botanists. Kleynhans *et al.'s* (2007) three lateral zones are:

- the marginal zone, akin to the wet bank and wet edge zones, which is expected to flood intra-annually;
- the lower zone, akin to the tree-shrub zone that incorporates the transition between the marginal and lower zones, which is expected to be located between the 1 and 3 year flood recurrence interval, and;
- the upper zone, akin to the back dynamic and outer transitional, is expected to be located outside of the 3-year recurrence interval.

2.3.2 Environmental flows and South African river management

Methods for assessing and monitoring river health and environmental flow requirements of rivers are based on assumptions about how changes to a natural flow regime affect the structure and functioning of an aquatic ecosystem, of which riparian vegetation forms one component, and tend to make use of lateral zone categorisations in the sampling protocol and interpretation of data. Methods of assessing river health are not particularly relevant to predictions about flow-linked changes in riparian vegetation communities, and so are not described further, although in many environmental flow studies the assessment of river health forms an integral component for the establishment of baseline conditions against which future states are monitored. A brief summary of the assessment of environmental water requirements is provided next, and particular focus is directed toward South Africa.

Environmental flows describe the pattern of flows (magnitude, timing, frequency, duration, variability and quality) both intra-annually and inter-annually of water required to sustain freshwater and estuarine ecosystems and the livelihoods of subsistence users that depend on these ecosystems (Hirji and Davis 2009, King *et al. in press*). Identifying flow components; such as the range of low flows in the dry and wet seasons; the size, numbers and timing of small floods; the size and timing of large floods, and; the temporal characteristics of the flow regime; and understanding the consequences of their loss, to the ecosystem under investigation, is central to a flow assessment (King *et al.* 2003).

Work on environmental flows began in the 1940s in western United States with simple hydrological approaches to determine minimum flows, usually at an annual, seasonal or monthly basis, for some ecological feature of a river ecosystem (Gordon *et al.* 1992). Further developments in the 1970s focussed on quantifying the relationship between the quantity and quality of an aquatic resource, such as seasonal changes in the distribution of flow-related fish habitat required for passage and spawning, with discharge (Tharme 2003). Since then, two approaches to flow assessments have developed; prescriptive, in which flows are described to achieve a narrow and specific objective; and interactive, which focus on changes in river flow and one or more aspects of the river to provide a range of options for river condition (Brown and King 2006). In South Africa, initial work in the 1990s led to the development, and use of, the BBM (Building Block Methodology, King and Louw 1998), a prescriptive approach that formed the basis of the determination of the Ecological Reserve (see below) in the South African National Water Act (King and Pienaar 2008). The BBM method was abandoned as the outcome did not lend itself to negotiation between water users nor provide sufficient information about the implications of not meeting the recommended values. Since then, two other interactive and holistic methods (Arthington *et al.* 1998) are in use in South Africa, DRIFT (Downstream Response to Instream Flow Transformation, King *et al* 2003) and the Flow Stressor-Response method (Hughes and Louw 2010). Both incorporate assessments of changes in a range of biophysical disciplines, such as hydrology, hydraulics, fluvial geomorphology, sedimentology, chemistry, botany and zoology; and socio-economic disciplines where there are subsistence users, such as sociology, anthropology, water supply, public health, livestock health and resource economics (King *et al.* 2003). The consequences of flow changes to riparian vegetation communities, for example, are predicted by understanding how flow influences riparian habitat and flora, based on assumptions about responses, such as; extreme floods reset physical river and riparian habitat (Naiman *et al.* 2008); medium floods flush riparian vegetation from the channel and small floods recharge groundwater for shallow rooted species (Naiman *et al.* 2000); normal low flows maintain the wet bank community (Boucher 2002); and drought lows enable recruitment and purge invasive riparian and aquatic species (Naiman *et al.* 2000).

Environmental flows were recognised as the foundation of integrated water-resources management (King and Pienaar 2011) during the writing of the South African National Water Act (Act 36 of 1998), which stipulated that water must be secured as a basic water supply to satisfy basic human needs and to protect aquatic ecosystems sustainably during water

resource development (NWA 1998). These two components were collectively called the Ecological Reserve and are stipulated in terms of quantity and quality of water required (King and Pienaar 2011). Determination of the Ecological Reserve for a water resource follows an eight step procedure (DWAF 1999) whereby the study area is delineated in terms of significant biophysical features; the present condition is determined, in terms of ecosystem health and importance; the ecological water requirements are calculated, using either the DRIFT or Flow Stressor-Response methods, and; the consequences of different operational scenarios determined on the available water resources (King and Pienaar 2011). The results are presented to the Department of Water Affairs Directorate: Resource Directed Measures (DWA D: RDM) who make a decision on the condition of the water resources that are to be maintained and then sign off on these preliminary reserves, which are legally binding and represent water quality and quantity parameters that must be adhered to. The next step is to calculate the Resource Quality Objectives (RQOs, DWA 2011), which are the requirements for agreed water quantity, quality, and the associated habitat and biotic integrity to maintain the agreed conditions. RQOs are defined in terms of EcoSpecs, descriptors of the ecosystem (or indicators) and Thresholds of Potential Concern (TPCs), points along a continuum of change for each EcoSpec, which may highlight the need for some action in response to a measured change in one of the indicators. EcoSpecs are recognised for major ecosystem components, including hydrology, geomorphology, water quality, riparian vegetation, macroinvertebrates and fish. The final step in this process is implementation of the reserve flows and any other mitigation measures as well as establishing a monitoring programme to monitor the EcoSpecs.

Most Reserves determined thus far are preliminary as they have been completed without consideration of the bigger basin wide water issues. This is because development and testing of the Water Resource Classification System (WRCS, Brown *et al.* 2007), designed to address this issue, has lagged behind that of the reserve determination procedures. The WRCS addresses the economic, social and ecological implications of various permutations of managing the basin-wide water resources in one of three classes; minimally, moderately and heavily used. The management class is set for separate river reaches throughout the basin and RQOs are provided for each, one of which is the Ecological Reserve. In this way, the WRCS establishes the boundaries of the volume, distribution and timing of the water needed for ecosystem maintenance for that river reach, and the amount of water potentially available for off-stream use.

Water resource management in South Africa is currently at a critical junction. For at least the last 20 years, DWA's Directorate: Resource Directed Measures (D: RDM) has focused on documenting the present state of aquatic ecosystem health and on making predictions about how that state may change with changes in the quantity and quality of water available for their maintenance in order to set the Ecological Reserve (DWAF 1999). In the Western Cape for example, Reserve determinations have been completed for all of the mainstem rivers and estuaries, and for many wetland/vlei systems (although these are lagging behind mainly because off a paucity of appropriate hydrological data). The D: RDM is now prioritising Classification, and the gazetting of Resource Quality Objectives (including the Ecological Reserve). This is likely to shift the focus of aquatic ecosystem protection from setting environmental water requirements to implementation, bringing with it a whole new set of challenges. Not the least of these will be increased pressure to defend the scientific basis on which the Reserve was set and to show that it is working through on-going monitoring programmes. Classification requires trade-offs for every kilometre of river reach, which is a complex undertaking that cannot be completed easily, especially with scant data. The employment of specialist teams to undertake the complicated site-specific assessments required to generate baseline data for a study, from which predictions about consequences of flow change are made and extrapolated basin-wide, is expensive and time consuming. Moreover, modelling of links between biophysical components of the aquatic ecosystem are restricted to the site of interest, due to unique factors about river channel structure and flow of a reach, as well as limited ranges of species selected for inclusion into the study.

Successful prediction of future consequences of flow change and monitoring those predictions requires a distinction between natural or anthropogenic, and flow-related or non-flow related changes in those systems. In rivers, for instance, changes in the position and extent of sandbars could occur naturally along with shifts in the species composition of aquatic biota during dry and wet cycles, around some dynamic equilibrium. On the one hand, understanding the natural and historic fluctuations within ecosystems (both in the short-term, e.g. seasonal, medium term, e.g. 10 year wet and dry cycles and/or the effects of fire, and in the long-term, e.g., climate change) is essential to provide the template against which data generated by monitoring programmes are assessed. On the other hand, the hypotheses used to predict flow-related change may themselves be open to challenge. For example, monitoring results from the Malibamatso River in Lesotho suggest that predictions made with respect to a decline in riparian vegetation downstream of Katse Dam have not materialized (Mentis and Ledger 2005). Added to this are the compounding effects of global events such as climate change, leading to changes in rainfall regime and hence water supply to aquatic ecosystems (both in terms of volume and distribution), and more localised non-flow related impacts such as fire, landuse changes and invasion by alien species.

Biological invasions represent the second largest threat (after habitat destruction) to global biodiversity (Richardson and van Wilgen 2004). Ecotones, such as riparian areas, are particularly sensitive to environmental change and invasion (Naiman and Decamps 1997; Tickner *et al.* 2001) due to being regularly subject to anthropogenic disturbances (Richardson *et al.* 2007), such as impounding and diversion of water, abstraction of water from alluvial aquifers, overgrazing by livestock, removal of trees for building and firewood, clearing of land for cultivation, mining, roads, recreational use and fire (Naiman *et al.* 2005). This vulnerability is heightened in semi-arid regions at least partly due to water being available in an otherwise dry landscape (Dye *et al.* 2001), but also because violent floods create patches of open sediment ideal for germination of hydrochorous seed (Knight 1985, Versfeld *et al.* 1998) – in particular invasive seed. In the process, indigenous vegetation communities are displaced and invasive species introduced and many riparian areas require sustained management to prevent re-invasion (Richardson *et al.* 1997).

One of the most contentious issues in South Africa is water use by woody invasives that are said to have considerably higher rates of transpiration (Dye *et al.* 2001), and thus use more water, than their indigenous counterparts (Dye and Poulter 1995; Versfeld *et al.* 1998). Different studies provide a range of estimates for reductions in river flow and thus water yields from basins based upon the degree to which natural vegetation guilds have been displaced. For example, reduction in river flows is estimated at 6-22% if indigenous forests are replaced by invasive trees, depending upon the species of invasive (Le Maitre *et al.* 2002), and up to 50% where grassland is replaced by invasive trees (van Wilgen and Richardson 2012). Rebelo (2012) estimated that clearing invasives from wetlands in the upper Kromme River and reinstating natural hydrological functioning of these wetlands would result in a 30% increase in mean annual runoff downstream. In South Africa, the impact of woody invasives on water availability was considered so severe that the Working for Water (WfW) programme was launched in 1998 to maximise the delivery of water resources, enhance sustainability by eliminating invasive species, and promote social equity through jobs and training for economically marginalised people (van Wilgen *et al.* 1995). Fifteen years on, WfW has cleared *ca.* 1,000,000 hectares of invasive species and estimates are that 9 – 10,000,000 remain (Koenig 2009). Restoring natural systems after invasion is a long process and is complicated in different regions by climate, landscape, the alien species present and the available native seed bank. Invasive seed banks are notoriously persistent (Holmes *et al.* 2005) and invasives recruit year after year of clearing, requiring a sustained effort in follow-up clearings. Significant progress has however been made in best practice of clearing methods and restoration techniques in different biomes around the country (Holmes *et al.* 2005, Blanchard and Holmes 2008, Vosse *et al.* 2008).

2.4 Conceptual framework

This dissertation investigated links between river flow and the structure of riparian vegetation communities. Flow is considered to influence the distribution of riparian plants in three main ways (Van Coller 1992):

- as a resource necessary for growth and reproduction;
- as an agent of disturbance (floods); and
- as a stressor during periods of prolonged low flow.

The central assumption is that vegetation zonation patterns along rivers result from differential species responses to a combination of abiotic factors that vary in space and time (Van Coller 1992). According to Kleynhans *et al.* (2007), a riparian zone consists of three lateral zones (Figure 2.1) bounded by a freshwater and terrestrial ecosystem on either side. Assumptions about how the influence of abiotic factors change between these three lateral zones are summarised in three categories: flow factors, patch factors and plant traits (Table 2.3). The conceptual framework is based on separating these assumptions out across the three lateral zones.

In general, water availability decreases laterally away from the river channel as the depth to groundwater increases and the frequency of flooding and inundation duration of flood events decreases (Naiman *et al.* 2005). Inundation duration influences vegetation structure, with permanent to frequently inundated areas generally dominated by herbaceous perennials and graminoids, while those less frequently inundated are dominated by shrubs and trees and an understory of herbaceous perennials and graminoids (Toner and Keddy 1997, 2006; Merrit *et al.* 2010). The combination of a decrease in water availability and in the frequency of being flooded equates to a higher probability of experiencing a water shortage higher up the bank.

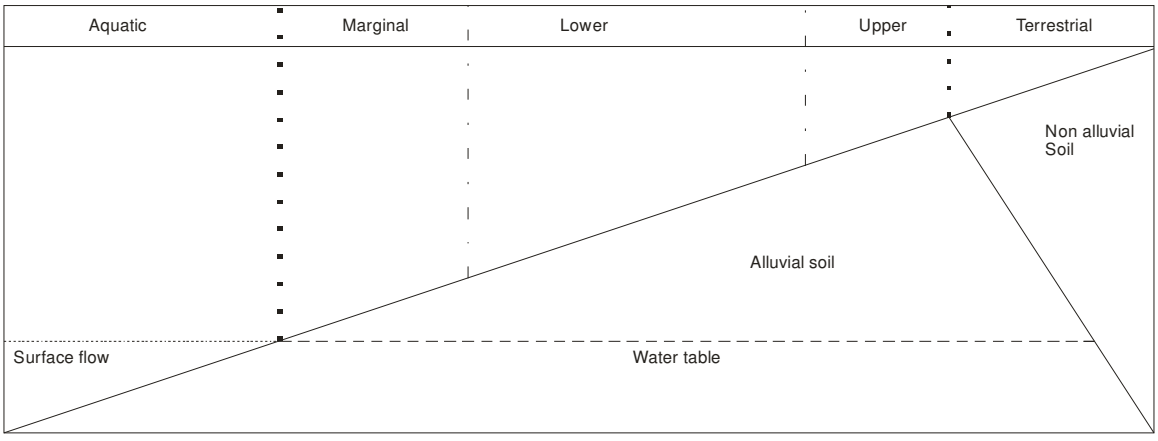

Figure 2.1 A schematic of the Kleynhans *et al.* (2007) riparian zones.

Table 2.3 Assumptions made with respect to the influence of abiotic factors in different lateral zones. BR -= bedrock.

Flow factors		Marginal zone	Lower zone	Upper zone	Reference
Surface flow	Maintenance	Base flows ↔ Inter-annual floods			Hupp and Osterkamp (2002)
	Disturbance	Intra-annual floods ↔ Inter-decadal floods			Boucher (2002)
	Periodicity	Annually regular ↔ Annually stochastic/decadally regular			Nilsson and Svedmark (2002)
Sub-surface flow	Water table	Permanent access ↔ Seasonal access			Castelli *et al.* 2000
Patch factors					Saxton and Rawls (2006)
	Substratum type	BR/alluvium ↔ Alluvium/colluvium			Moon *et al.* (1997)
	Stability	Stable/mobilised ↔ Increasing stability			Hupp and Osterkamp (1996)
	Hydraulic conductivity	High ↔ Low			Brady and Weil (1999)
	Soil nutrients	Low ↔ High			Saxton and Rawls (2006)
Plant traits					
	Growth rate	High ↔ Low			Hemphill (1998)
	Water use efficiency	Low ↔ High			Keeley (1979)
	Flood tolerance	High ↔ Low			Karrenberg *et al.* (2002)
	Drought tolerance	Low ↔ High			Borchert (1994)

Since plants in the marginal zone are inundated annually (Kleynhans *et al.* 2007), it is expected that the duration of inundation under high flow is greater for plants in the marginal zone than for plants in the lower or upper zones. Fluvial sediments are regularly washed, frequently mobilised and do not offer a stable surface for colonisation (Hupp and Osterkamp 1996). If the channel is bedrock controlled however, a stable bedrock pavement may be available and certain specialist plants, such as the perennial tree *Breonadia salicina,* are adapted to this niche (van Coller 1992). Being regularly disturbed and wet, plants in this zone have high growth rates and low water use efficiencies (Stromberg 2001). In the same way, plants of the marginal zone have a high tolerance to flooding and correspondingly a low tolerance to drying out. Being in such close proximity to water it is expected that marginal plants would be predominantly hydrochorous[10] although alternative mechanisms of seed dispersal may also occur. Many marginal zone species are soft-stemmed or fleshy, and bend easily if inundated by floods (Karrenberg *et al.* 2002), thus may easily suffer stem snap, be uprooted or broken into fragments during periods of high flow (Naiman and Decamps 1997). Some clonal species disperse vegetative fragments (diaspores) that take root on new sediment deposits (Nilsson 2002). Any terrestrial species colonising this zone are expected to be drowned due to an oversupply of water.

The lower zone is comprised of a mixture of alluvium and colluvium (Francis 2006), which offers a more stable landform for colonisation and is inundated less regularly by floods (1-3 years; Kleynhans *et al.* 2007). Thus, plants in this zone are expected to be more tolerant to drying out, reflected in lower growth rates and higher water use efficiencies (Swift *et al.* 2008), than those in the marginal zone.

Plants in the upper zone are inundated less regularly by floods that recur > 3 years, compared with those occupying the lower zone. Thus, for plants in the upper zone, tolerance to drying could be of critical importance to survival (Gasith and Resh 1999), particularly during the dry season. This is a transitional zone (Kleynhans *et al.* 2007), so the more drought tolerant lower zone species will be found here along with other terrestrial species that are intolerant to flooding. Factors other than river flow are expected to play an increasingly important role in the life histories of upper zone occupants (Francis 2006) and hence the links to river flow are expected to be considerably weaker than for the marginal and lower zones.

[10] Regenerate by water dispersed seed.

Thus, the life history strategies of species occupying the marginal, lower and upper zones are expected to differ. The life histories of marginal zone plants are expected to be more intimately linked with the flow regime than upper zone plants although the roles of density dependence, competition and other interactions between riparian plants and of water availability on establishment and persistence are not well understood. There is a paucity of data on the prevalence of seed dormancy, germinability, propensity to form seed banks, the rooting depth of adults, phenology (flowering and seed set), resistance to floods and resilience during droughts. We need to know more about the modes of reproduction of riparian plants and factors controlling their dispersal in order to formulate better predictions about the consequences of alterations to flow, upon which many of these factors rely. There is a need to better understand natural fluctuations within river ecosystems and to be able to separate these from anthropogenic driven changes, both which may be flow or non-flow related. A better understanding of riparian community structure will facilitate this as it can provide a framework within which we may contextualise consequences and species responses, in particular with respect to the role of invasives and restoration following clearing. If a generic riparian community structure is applicable to different rivers and community types, the understanding of the mechanisms responsible for the inherent structure could lead to generic rules about flow and riparian community functioning that transcend riparian community type or river channel topography. This will greatly aid management of rivers in general and particularly communities downstream of dams by providing a basis for generic release patterns.

3 Lateral zones in Fynbos Riparian Vegetation

This paper was presented at the Young Water Professional's conference in July 2013. Karen Esler, Cate Brown and Jackie King are co-authors as each contributed towards the concepts therein and reviewed the manuscript. Martin Kidd assisted with statistical analyses.

With regard to the sections listed below, the nature and scope of my contribution were as follows:

Section	Page number	Nature of contribution	Extent of contribution
3.2.2.2	28	Data analysis	75%
3.2.2.3	28	Data analysis	80%
3.3.3.1	38	Results from analysis	95%

The following co-authors have contributed to the sections listed below:

Co-author	Email	Section	Nature of contribution	Extent of contribution
M Kidd	mkidd@sun.ac.za	3.2.2.2	Data analysis	25%
M Kidd		3.2.2.3	Data analysis	20%
M Kidd		3.3.3.1	Results of analysis	5%

Signature of candidate:

Date: 23 October 2013

The undersigned hereby confirm that:

1. The declaration above accurately reflects the nature and extent of the contributions of the candidate and the co-authors in the listed sections,
2. No other authors contributed to the listed sections besides those specified above, and
3. Potential conflicts of interest have been revealed to all interested parties and that the necessary arrangements have been made to use the material in the listed sections of the dissertation.

Co-author	Signature	Institutional affiliation	Date
Martin Kidd		University of Stellenbosch	

3.1 Introduction

Perennial south-western Cape headwater streams are lined by Fynbos Riparian Vegetation (Mucina and Rutherford, 2006), which dominates rivers in valleys with fire cycles shorter than 50 years and is typified by the small trees *Brabejum stellatifolium, Metrosideros angustifolia* and *Brachylaena neriifolia* (Holmes *et al.* 2005). Despite extensive research in the Fynbos biome of the south-western Cape, a Mediterranean Type Ecosystem (Cowling *et al.* 2004), the structure of riparian vegetation communities has not been intensively studied until recently (Prins *et al.* 2004; Sieben and Reinecke 2008; Sieben *et al.* 2009; Meek *et al.* 2013). Indeed, there are few formal classifications of South African riparian vegetation in general, although some work has been done in the floodplain forests of the Savanna Biome in the north of the country (van Coller 1992; Moon *et al.* 1997; Parsons *et al.* 2005; van Coller *et al.* 1997, 2000). Classifications of Fynbos Riparian Vegetation have tended to either incorporate generalist species useful for restoration targets (Prins *et al.* 2005; Meek *et al.* 2013) or take the opposite approach by separating out generalists from discriminant species in order to name distinct communities (e.g., Sieben 2002; Sieben and Reinecke 2008; Sieben *et al.* 2009). The former are based on large plots (> 50 m^2) of the riparian area and tend not to sub-divide these into lateral zones. The latter are phytosociological studies, such as the Braun-Blanquet classification system (Werger 1974), which rely on the *a priori* identification of lateral zones, and employ sampling techniques that avoid transitions between zone types.

Most of these phytosociological studies in the Western Cape make use of Boucher's (2002) seven-zone classification system to distinguish zones.

Regardless of the methods applied to identify and study them, the use of zonal descriptions demonstrates the belief that lateral zones exist, and that they are linked in some way to changes in bank topography, aspects of the flow regime or a combination thereof (Chapter 2). There is, however, less agreement on the number of zones, or whether zonal patterns are comparable across river basins. This uncertainty may stem from differences in sampling methods, data analysis and interpretation, which make it difficult to reach consensus on the zones that occur. Most studies assume the existence of pattern and accommodate this into the sampling protocol, usually by delineating *a priori* sample plots within community types (Boucher 2002; Sieben 2002; Blanchard and Holmes 2008; Vosse *et al.* 2008; Jacobs *et al.* 2013). This approach is based on assumptions of community stability at larger scales such as those for terrestrial ecosystems and may be unsuitable for use in relatively variable, narrowly-linear environments (Kent and Coker 1992), such as riparian areas. The main confounding issue with phytosociological data is that because the boundaries between lateral zones are selected upfront, different practitioners can produce different classifications for the same site. Further problems arise during data processing. Data reduction techniques are used to compare species abundance between samples that were allocated to lateral zones *in situ*. If however, after analysis, a sample is shown to be more closely related to a different lateral zone, the position of that sample may either be moved back to the pre-allocated lateral zone or the assigned zone type changed. This decision-making process creates a circular argument in the allocation of samples to lateral zones.

There are two generally upheld classifications for riparian vegetation in South Africa. The first, more comprehensive is that of Boucher (2002), which describes seven lateral zones said to be correlated with flood recurrence intervals (see Chapter 4; Sieben 2002; Sieben and Reinecke 200; Sieben *et al.* 2009). The second, more recent, classification was developed by a group of South African botanists for the Vegetation Response and Assessment Index (VEGRAI, Kleynhans *et al.* 2007), and describes three lateral zones loosely linked to flood recurrence intervals and bank shape.

The objective of this chapter was to test whether the generic pattern described by Kleynhans *et al.* (2007) is present in Fynbos Riparian Vegetation. If so, the next logical step would be to test whether the same pattern may be found in other types of riparian communities outside of the Fynbos biome that differ in species present, seasonal rainfall and flow regime (see Chapter 4). If that was also shown to be true, this could lead to an explanation for the pattern of zones, which could enhance understanding of their nature, location and functioning.

Headwater streams are well-suited to the study of riparian zonation patterns as the communities are laterally constrained and the lateral gradients are steep (Gomi *et al.* 2002). Reinecke *et al.* (2007) did preliminary analyses of patterns of zonation in Fynbos Riparian Vegetation and reported evidence of four lateral zones. However, the analyses used cover abundance scores of species rooted outside of the sample area, which may have skewed the results as riparian species can also grow laterally, and a plant may be rooted 5 to 10 m away from its canopy. In this study, plants were recorded according to the sample plot they were rooted in, and methods of data collection and analysis were chosen that allowed identification of patterns of plant distribution that were guided by the data rather than by pre-selection of zones. Thus, if patterns were found, then the work could be repeated in other hydrogeomorphical settings and for other kinds of riparian vegetation communities, ultimately contributing toward a refined framework for identifying zone types.

The key question in this chapter (Figure 1.1) was, "Can characteristic species/taxa be used to identify lateral riparian zones?" This was examined through testing two hypotheses:

- Riparian plants are distributed in a repetitive and predictable manner.
- Characteristic plant taxa are restricted to specific lateral zones.

3.2 Methods

3.2.1 Data collection

Data were collected from 16 sites on five reference rivers in the Fynbos biome (Table 3.1). A geomorphological hierarchy (Rowntree *et al.* 2000; Chapter 2) was used to classify the longitudinal zone in which each site was located based upon river slope and valley shape (Table 2.1). Slope was calculated from electronic 1:50 000 maps in QGIS (V 1.4.0, 2010). Headwater sites, in the mountain stream, transitional and upper foothills zones, were chosen on single thread rivers with restricted floodplain development and predominantly longitudinal river flow.

At each site four contiguous belt transects were laid out (Figure 3.1). Cover abundance data, estimated visually as a percentage of each plant species in each sample plot, were collected for all tree and non-tree species rooted in the sample plots. Species presence/absence across sites are provided in Appendix Table 8.1. Only cover of species rooted in the sample plot were included in cover estimates. Transects, which comprised contiguous 5x1 m sample plots were positioned from the water's edge to the outer edge of the riparian zone, as indicated by the presence of terrestrial vegetation. The density and distribution of trees and shrubs were recorded to 1 m accuracy within each sample plot. Trees were separated into three life history stages; seedlings (height <0.3 m), saplings (0.3 < height < 2 m) and adults (height > 2 m).

Table 3.1 Location and description of study sites. mAsl = metres above sea level. Zones as per Rowntree *et al.* (2000, Table 2.1).

Basin	River	Code	Longitudinal zone	Gradient	Altitude (mAsl)	Co-ordinates
Olifants	Rondegat	R1	Mountain stream	0.085	624	S 32.396067°, E 19.089733°
		R2	Mountain stream	0.085	624	S 32.396033°, E 19.089467°
		R3	Transitional	0.029	501	S 32.376825°, E 19.067119°
		R4	Transitional	0.029	497	S 32.376325°, E 19.066775°
	Heks	H1	Transitional	0.023	245	S 32.435379°, E 19.008838°
		H2	Transitional	0.023	244	S 32.435269°, E 19.008638°
		H3	Upper Foothills	0.018	175	S 32.436450°, E 18.981384°
		H4	Upper Foothills	0.018	167	S 32.436533°, E 18.981342°
Breede	Witte	W1	Transitional	0.027	285	S 33.571850°, E 19.138617°
		W2	Transitional	0.027	281	S 33.571550°, E 19.138717°
	Elands	E1	Mountain stream	0.054	519	S 33.760900°, E 19.128417°
		E2	Mountain stream	0.054	505	S 33.760753°, E 19.128325°
		E3	Transitional	0.017	450	S 33.740167°, E 19.113183°
		E4	Transitional	0.017	446	S 33.739756°, E 19.113142°
Berg	Jonkershoek	J1	Mountain stream	0.040	360	S 33.993750°, E 18.975517°
		J2	Mountain stream	0.040	314	S 33.987075°, E 18.956507°

The location (elevation and distance from the water's edge) of each sample plot was surveyed with a total station (Leica TC307 model). Four cross-sections were surveyed from upper bank to upper bank through the channel; each was located in the middle of a belt transect. Soil particle size was recorded for each sample plot using the Wentworth scale (Gordon *et al.* 1992). Collected plant specimens were identified by the Compton Herbarium, located at the Kirstenbosch National Botanical Gardens, Cape Town, South Africa. Species were assigned to one of 11 growth form categories following descriptions from Goldblatt and Manning (2000). For the purposes of the analyses that follow, trees and small trees were combined into a tree category, and all other growth forms were combined in a non-tree category.

Table 3.2 Growth form definitions (Goldblatt and Manning 2000).

Growth form	Definition
1 forb	A broad leafed herbaceous plant.
2 geophyte	A perennial plant that propagates by underground bulbs or tubers or corms.
3 rhizomatous perennial	Plants in the division Pteridophyta.
4 rush	Plants in the family Juncaceae.
5 sedge	Plants in the family Cyperaceae.
6 grass	Plants in the family Poaceae.
7 restio	Plants in the family Restionaceae.
8 small shrub	A low woody perennial plant often with multiple stems (<1m).
9 shrub	A medium sized woody perennial plant often with multiple stems (1-2m).
10 small tree	A large woody perennial plant usually with multiple stems (2-10m).
11 tree	A tall woody plant with main trunk, branches and a distinct elevated crown (>10m).

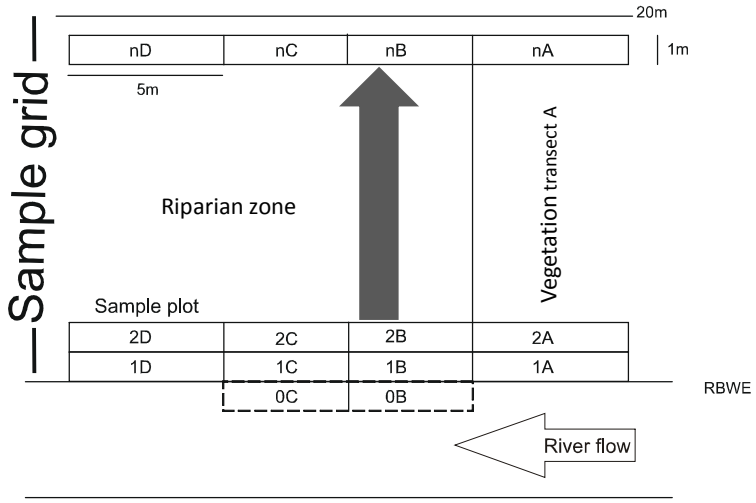

Figure 3.1 Sample grid of belt transects, showing vegetation transects A to D. RBWE = right bank water's edge. Sample plot codes (e.g. 2B = metre 2 transect B), measured from the wetted channel edge.

3.2.2 Data analyses

The data were analysed at two scales: *between* rivers at a site-scale and *within* sites at the sample-plot scale. For the river comparisons, cover abundance data from all sample plots at a site were lumped together by summing cover values into a single species list for each site. For both sets of analyses, multivariate analyses (PRIMER V6, Clarke and Warwick 2006) were used to discern patterns of zonation based on species–level similarities between groups. Data were 4^{th} root transformed in order to boost the presence of smaller species at lower covers. Bray-Curtis similarity coefficients were calculated between groups and the results were displayed using Multidimensional Scaling ordinations (MDS) and CLUSTER analyses (Clarke and Gorley 2006). ANOSIM (analysis of similarities, Clarke and Warwick 2001), a non-parametric permutation procedure analogous to ANOVA was used to determine significance of separation between groups. The SIMPER (similarity percentages) routine in PRIMER (V6, Clarke and Warwick 2006) was used to discern typical and differentiating species between groups and the results were tabulated.

3.2.2.1 Assigning names to the lateral zones

The different ways that tree and non-tree species contributed to the pattern were explored using the Rondegat River sites (R1 – R4, Appendix Figure 8.1 - Figure 8.4). Based on the results of this initial analysis it was decided to pursue the pattern by using the entire species complement, a combination of the tree and non-tree data. Lateral zones were assigned according to the following protocol. Groups of sample plots with greater than 40% similarity were tentatively recognised, along with a few clusters of plots with lower similarity but obvious cohesion as a group. A group was designated to a lateral zone based on the habitat characteristics of the dominant species'. Goldblatt and Manning (2000) provided habitat preference data (see Appendix Table 8.2) and plants were assigned to one of three categories as follows:

- species common on or near seeps, rivers and watercourses were deemed **obligate** riparian (wet) species;
- those occurring on rocky slopes and outcrops or mountain slopes were deemed **incidental** terrestrial (dry) species; and
- species described as occurring in bush, woodland or forests and/or associated with water courses were deemed **facultative** riparian (wet/dry) species.

The following logic was used to designate groups into lateral zones, using a combination of the Kleynhans *et al. (*2007) and Boucher (2002) names, based on which of the three categories of plants were dominant in a group:

- groups that contained only incidental species were designated terrestrial and were not considered further;
- groups containing a mixture of incidental and facultative species, and most closely related to the terrestrial group were designated *upper* zone;
- groups with facultative species were designated *lower* zone;
- groups with a mixture of facultative and obligate and most closely related to the lower or marginal groups were designated *lower dynamic* zone; and
- groups with obligate species were designated *marginal* zone.

3.2.2.2 Determining indicators for each lateral zone

General Discriminant Models (GDA, StatSoft 2013) were computed between the species composition of lateral zones for all rivers by combining the data from all sites but separating the data into three sub-sets, one for trees, one for non-trees and a combined set of the entire species complement. These GDA models listed the species most strongly associated with each lateral zone. These were selected as discriminating species and the average abundances of the indicator species in each lateral zone at all the sites were standardized, combined and their distribution across the four lateral zones plotted using bar graphs.

3.2.2.3 Developing rules about lateral zone distribution

The BIOENV routine in PRIMER (V6, Clarke and Warwick 2006) was used to determine which biophysical data (elevation, distance, soil depth, sediment calibre and proximity to water in wetted channel) best explained lateral species composition. A Classification and Regression Tree (C&RT, StatSoft 2013) was employed (Breiman *et al.* 1984) to determine physical rules for locating assemblage types. The predictor variables tested were: distance from summer low-flow water's edge; elevation from summer low-flow water's edge; wet Bank (WB) gradient 1, over the first three sample plots (from wetted channel edge upwards); dry Bank (DB) gradient 2, covering sample plots four to six (4 - 6 m distance from water's edge up the bank); bank shape, the difference between gradients 1 and 2 (a negative value indicated a concave bank and positive value a convex bank); whether the river bank overall was convex or concave; gradient 3, over the last three sample plots (the steeper this gradient

the narrower the valley); percentage of sand per sample plot; and percentage of surface water per sample plot. A C&RT creates a decision tree that designates a dependent variable, in this case the lateral zone, to a sample plot based on the best fit about a range of independent variables; in this case the predictors listed above. Seventy percent of the sample data were selected at random to represent the *observed* set for model development, the remaining 30% were the *test* set used to ascertain the predictive accuracy of the prescribed rules.

3.3 Results

3.3.1 River comparisons

The 16 sites first grouped by river basin. The Hex and Rondegat Rivers of the Olifants River Basin separated from the Witte and Elands Rivers of the Breede River Basin, while the Jonkershoek River formed a third group of the Berg River Basin (Figure 3.2). Within each basin group, the rivers separated from one another and replicate sites separated into longitudinal zones. For example, the two transitional sites on the Hex River (H1 and H2) separated from those in the upper foothills (H3 and H4). This was true for all sites, rivers and basins.

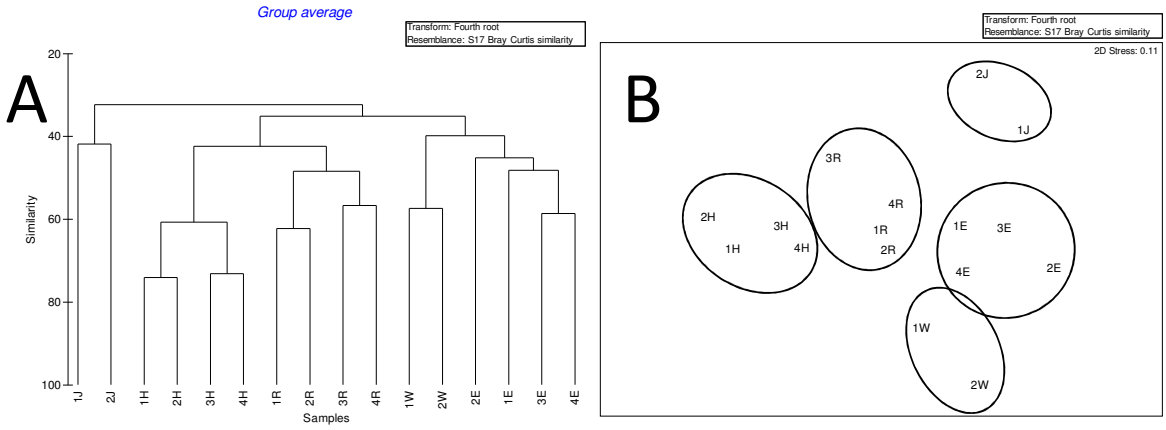

Figure 3.2 (A) CLUSTER and (B) MDS ordination of Bray Curtis similarity between species composition of sites. Site codes as per Table 3.1.

A global nested pair-wise ANOSIM of species abundances between sites (PRIMER V6, Clarke and Warwick 2006) showed that rivers were different ($R = 0.869$, $p < 0.01$). Thus, interpretations of patterns within the data were focussed at a river scale.

3.3.2 Typical and differentiating species for lateral zones

There were four kinds of lateral zones (Figure 3.3 - Figure 3.7). The marginal zone was situated at the wetted channel edge for a short distance up the bank. The lower zone formed the body of the riparian area and the upper zone formed the boundary with the adjacent terrestrial community. The fourth lateral zone, the lower dynamic, was transitional between the marginal and lower and could be most similar to either, depending upon whether it comprised obligate or facultative riparian species. The majority of the riparian area comprised the lower and upper zones. In some cases a lateral zone was absent. For example, the marginal zone was absent alongside pools, such as at 2R, 4R, 4E and 1J. The upper zone was absent at 4R as the site was too laterally extensive to reach the adjacent terrestrial community using a contiguous sample plot layout. In all other cases there were four zones. The outputs of the CLUSTER and MDS ordinations concur on the pattern and this was taken to strengthen the relationships presented (Clarke and Warwick, 2006).

The SIMPER analyses revealed that the marginal zones on the Hex and Rondegat Rivers were dominated by *Isolepis prolifera,* while at the Elands River *Salix mucronata* and *Prionium serratum* were more common (Table 3.3). The marginal zone at the Witte River was dominated by saplings of *Morella serrata* and *Brachylaena neriifolia.* The most common plants in the lower dynamic were *Calopsis paniculata,* at the Rondegat and Hex Rivers, and trees and saplings of *Morella serrata,* at the Elands, Witte and Jonkershoek Rivers. *Erica caffra* was also typically found in the lower dynamic zone of the Rondegat and the Jonkershoek Rivers. The tree *Metrosideros angustifolia* was the most common lower zone plant at the Rondegat, Hex, Witte and Elands Rivers but not at the Jonkershoek River. Some plants typically found in the lower dynamic were also present here, including *Morella serrata, Erica caffra* and *Elegia capensis.* The upper zone comprised species typical of disturbed areas, such as *Pteridium aquilinum,* or incidental species such as *Ehrharta ramosa, Ehrharta rehmannii, Pentameris distichophylla* and *Diospyros glabra.* The degree of similarity between species abundances between groups ranged from 9-60% reflecting a wide variance in the distribution of plants between lateral zones and between sites.

SIMPER showed that *Isolepis prolifera* was a good differentiating species for the marginal zone at the Rondegat and Hex Rivers (Table 3.4). Saplings of *Morella serrata* and *Salix mucronata* were good differentiators for the Witte and the Elands River respectively. There was no marginal zone at the Jonkershoek River. *Calopsis paniculata* was a good differentiating species for the lower dynamic at the Rondegat and Hex Rivers while *Elegia capensis,* another restio, was situated in this position on the Elands River. Saplings of *Metrosideros angustifolia* and *Brabejum stellatifolium* were good differentiators for the lower zone at the Witte and Jonkershoek Rivers respectively.

The tree *Metrosideros angustifolia* was a good differentiator for the lower zones of the Rondegat, Hex, Witte and Elands Rivers, along with the tree *Brabejum stellatifolium* at the Rondegat and Jonkershoek Rivers. Incidental grasses, such as *Ehrharta ramosa, Ehrharta rehmannii* and *Pentameris distichophylla* were good differentiators for the upper zone, as were incidental trees *Maytenus oleoides* and *Hartogiella schinoides* on the Witte as well as the shrub *Diospyros glabra* on the Heks River. In some cases a plant, for example the tree *Morella serrata*, was a good differentiating species for two different zones; the lower zone at the Hex River and the lower dynamic at the Jonkershoek River.

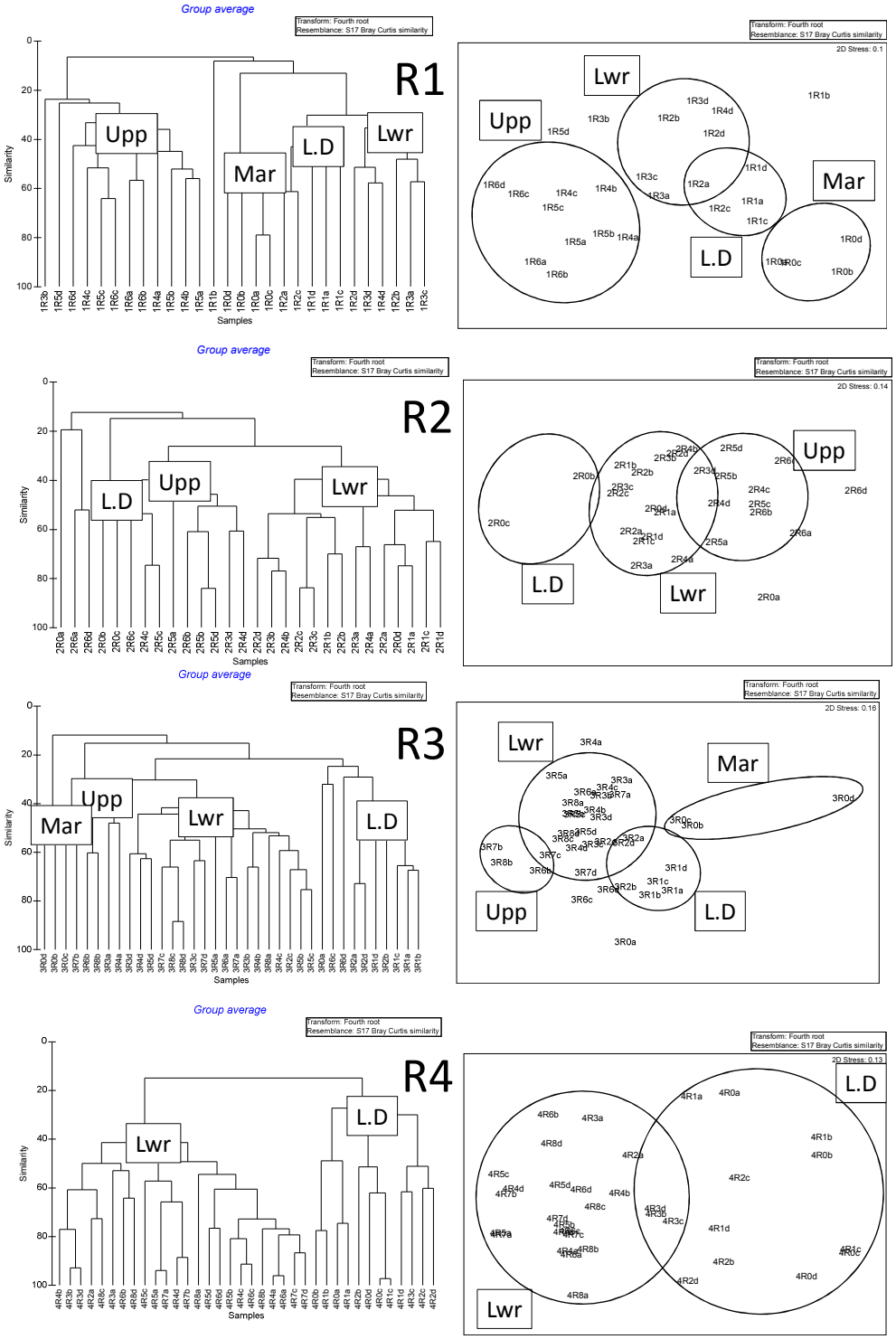

Figure 3.3 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on the Rondegat River. Mar = marginal, L.D. = lower dynamic, Low = lower and Upp = upper. Sample plot codes as per Figure 3.1. Site codes as per Table 3.1.**

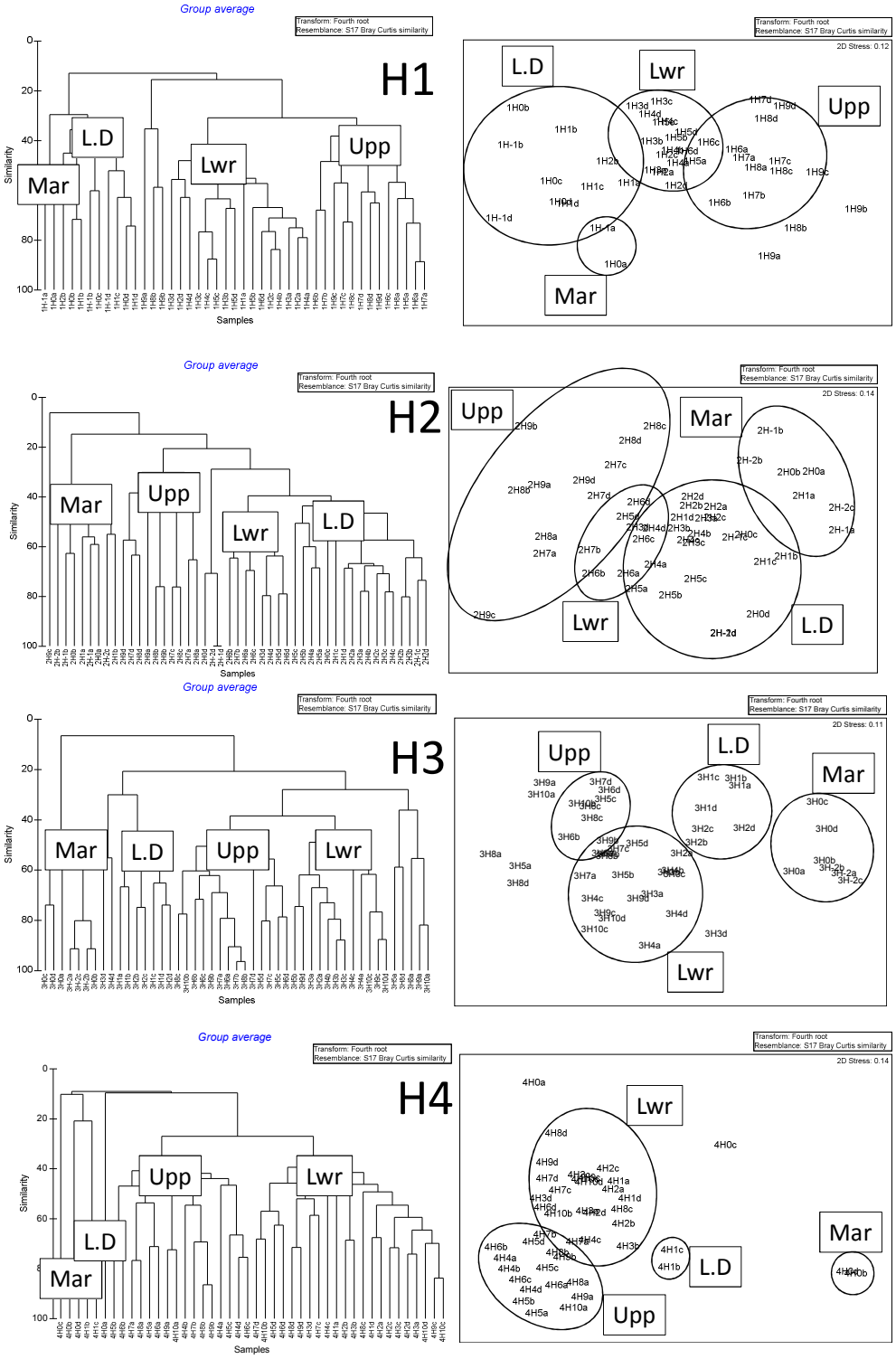

Figure 3.4 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on the Hex River. Mar = marginal, L.D. = lower dynamic, Low = lower and Upp = upper. Sample plot codes as per Figure 3.1. Site codes as per Table 3.1.**

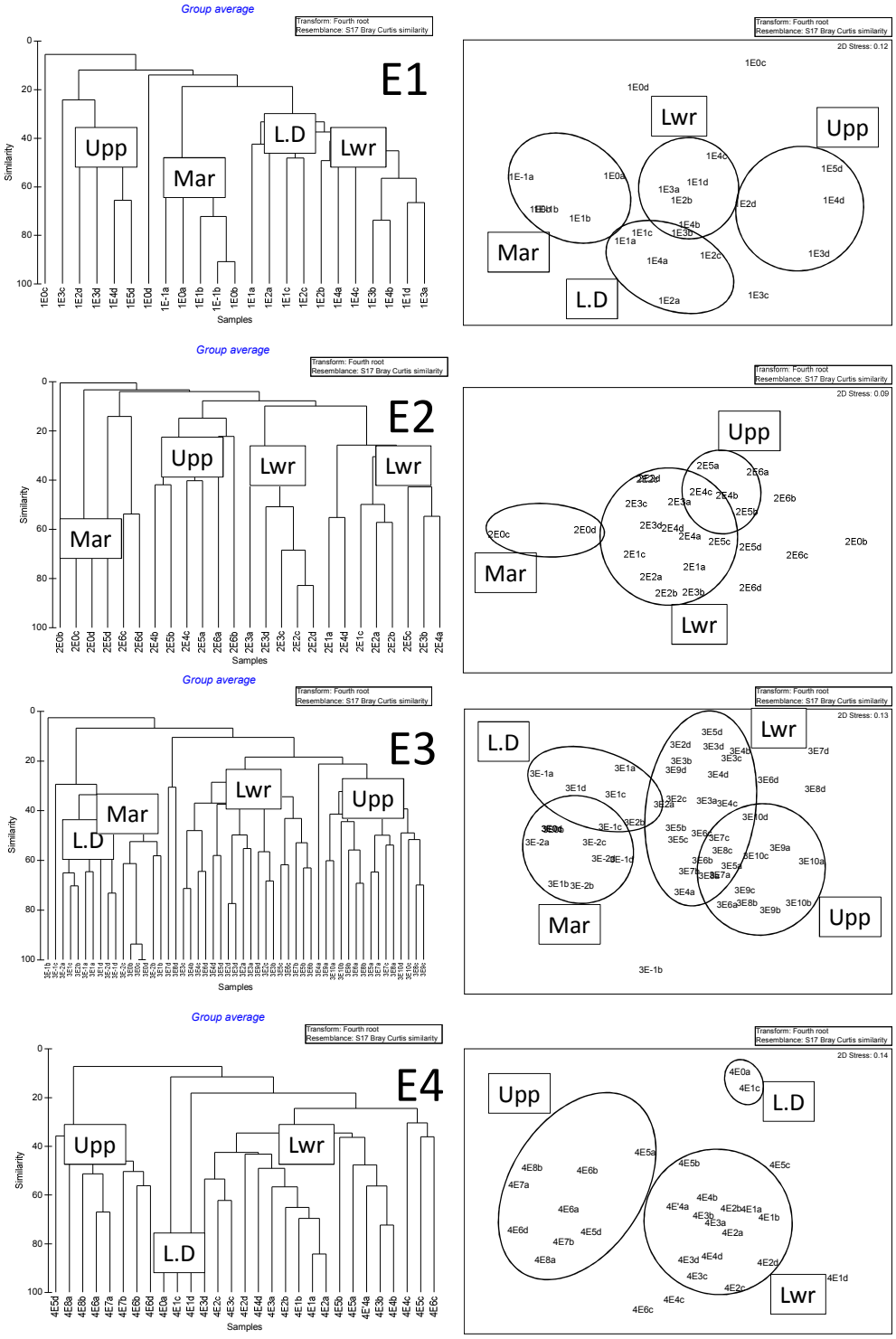

Figure 3.5 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on the Elands River. Mar = marginal, L.D. = lower dynamic, Low = lower and Upp = upper. Sample plot codes as per Figure 3.1. Site codes as per Table 3.1.**

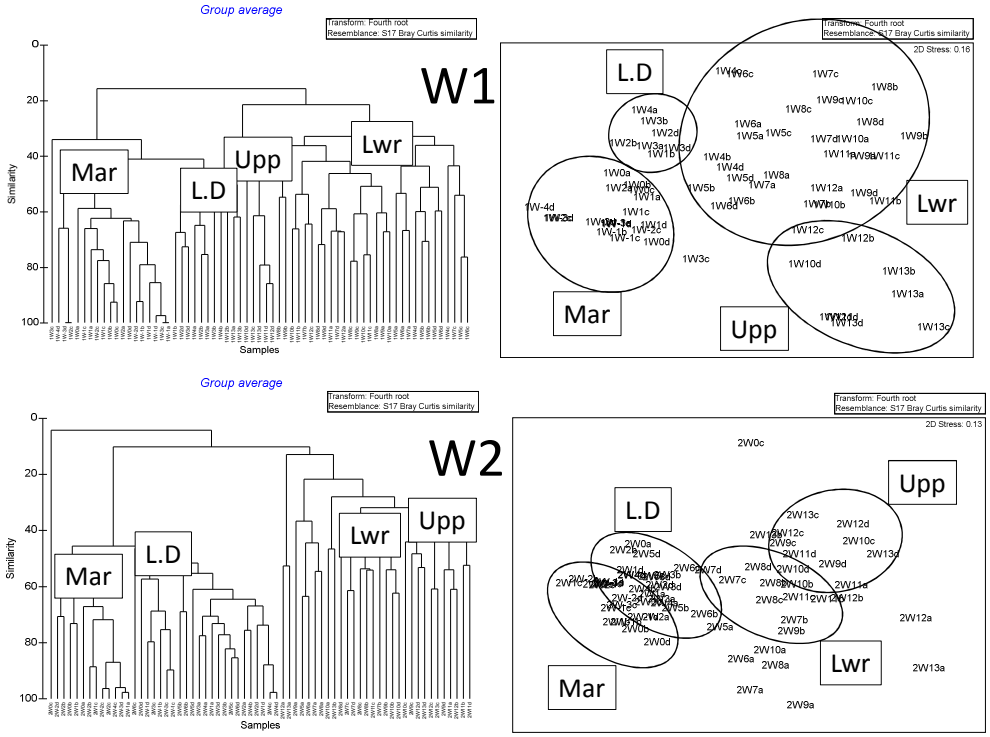

Figure 3.6 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on the Witte River. Mar = marginal, L.D. = lower dynamic, Low = lower and Upp = upper. Sample plot codes as per Figure 3.1. Site codes as per Table 3.1.**

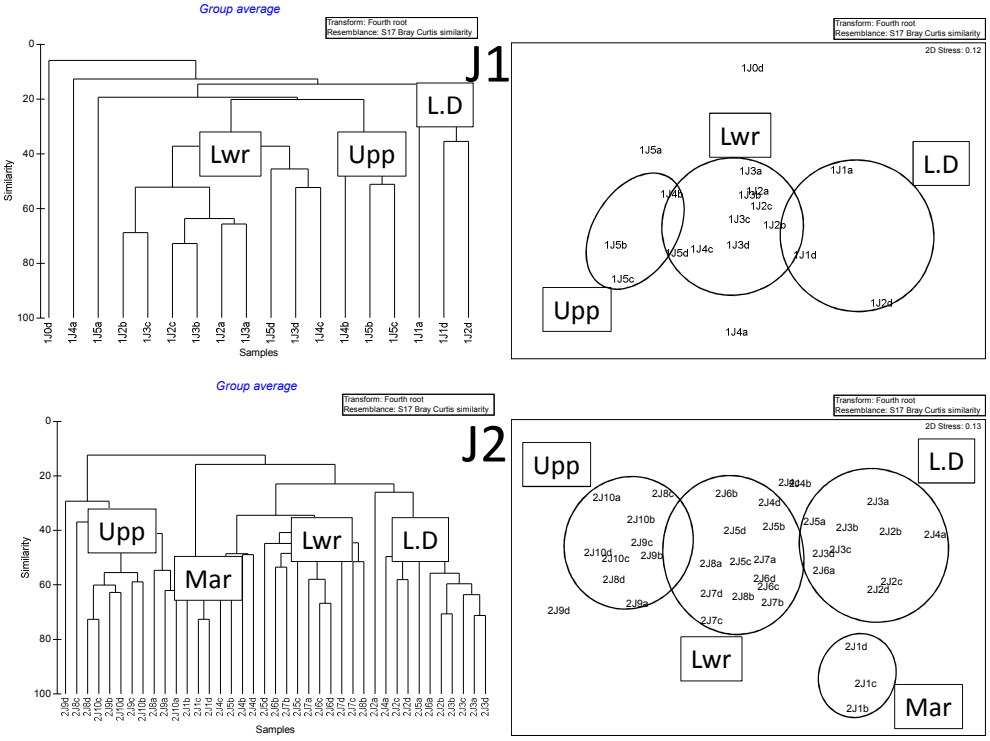

Figure 3.7 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on the Jonkershoek River. Mar = marginal, L.D. = lower dynamic, Low = lower and Upp = upper. Sample plot codes as per Figure 3.1. Site codes as per Table 3.1.**

Table 3.3 Typical species for lateral riparian zones per river. Sim = similarity coefficient. S = seedling, J = sapling and T = tree.

	Rondegat	Heks	Witte	Elands	Jonkershoek
Marginal	Sim = 51% *Isolepis prolifera*	Sim = 36% *Calopsis paniculata* *Isolepis prolifera*	Sim = 21% *Morella serrata J* *Brachylaena neriifolia J*	Sim = 24% *Salix mucronata J, S* *Prionium serratum*	Sim = 60% *Sphagnum sp.*
Lower dynamic	Sim = 28% *Calopsis paniculata* *Erica caffra*	Sim = 34% *Calopsis paniculata* *Morella serrata T*	Sim = 52% *Morella serrata J* *Metrosideros angustifolia J*	Sim = 25% *Elegia capensis* *Morella serrata S*	Sim = 35% *Erica caffra* *Morella serrata T*
Lower	Sim = 35% *Metrosideros angustifolia T* *Brabejum stellatifolium T*	Sim = 35% *Metrosideros angustifolia T* *Morella serrata T*	Sim = 30% *Metrosideros angustifolia T* *Morella serrata J*	Sim = 22% *Elegia capensis* *Metrosideros angustifolia T*	Sim = 32% *Erica caffra* *Sphagnum sp.*
Upper	Sim = 24% *Pteridium aquilinum* *Ehrharta ramosa*	Sim = 35% *Diospyros glabra* *Ehrharta rehmannii*	Sim = 9% *Brachylaena neriifolia J*	Sim = 20% *Pentameris distichophylla* *Pteridium aquilinum*	Sim = 36% *Pteridium aquilinum* *Calopsis paniculata*

Table 3.4 Differentiating species for lateral zones per river. J = sapling and T = tree.

	Rondegat	Heks	Witte	Elands	Jonkershoek
Marginal	*Isolepis prolifera*	*Isolepis prolifera*	*Morella serrata J*	*Salix mucronata J*	
Lower dynamic	*Erica caffra* *Calopsis paniculata*	*Panicum schinzii* *Calopsis paniculata*	*Metrosideros angustifolia J* *Morella serrata J*	*Elegia capensis*	*Brabejum stellatifolium J* *Morella serrata T*
Lower	*Metrosideros angustifolia T* *Brabejum stellatifolium T*	*Metrosideros angustifolia T* *Morella serrata T*	*Metrosideros angustifolia T*	*Metrosideros angustifolia T*	*Brabejum stellatifolium T* *Elegia capensis*
Upper	*Pteridium aquilinum* *Ehrharta ramosa*	*Diospyros glabra* *Ehrharta rehmannii*	*Maytenus oleoides* *Hartogiella schinoides*	*Pentameris distichophylla*	*Pteridium aquilinum* *Pellaea pteroides*

3.3.3 Indicators for lateral zones

The General Discriminant Analyses confirmed that some of these species were indeed useful indicators for lateral zones overall. Non-trees (Figure 3.8) and trees (Figure 3.9) were analysed separately and then combined (Figure 3.10).

Of the non-tree indicators (Figure 3.8), the most useful were *Prionium serratum* for the marginal zone, *Calopsis paniculata* and *Panicum schinzii* for the lower dynamic zone, *Elegia capensis* for the lower zone and *Pteridium aquilinum* and *Diospyros glabra* for the upper zone.

The abundance of saplings and trees did not coincide with each other (Figure 3.9). The tree *Metrosideros angustifolia* was most abundant species at all sites and in lower zone, while saplings were to be found in all four lateral zones although they were most common in the lower dynamic. Two of the other trees, *Brabejum stellatifolium* and *Brachylaena neriifolia* were also most common in the lower zone, while saplings of both were found in all four zones but were also most common in the lower dynamic zone. *Morella serrata* was most common in the lower dynamic zone and preferentially recruited there, although saplings were found throughout.

Overall, the best indicators for the four lateral zones, using a combination of trees and non-trees were (Figure 3.10):

- *Prionium serratum* and *Isolepis prolifera* for the marginal zone;
- *Calopsis paniculata* and *Morella serrata* trees for the lower dynamic zone;
- *Metrosideros angustifolia* trees and *Elegia capensis* for the lower zone; and
- *Diospyros glabra* and *Pteridium aquilinum* for the upper zone.

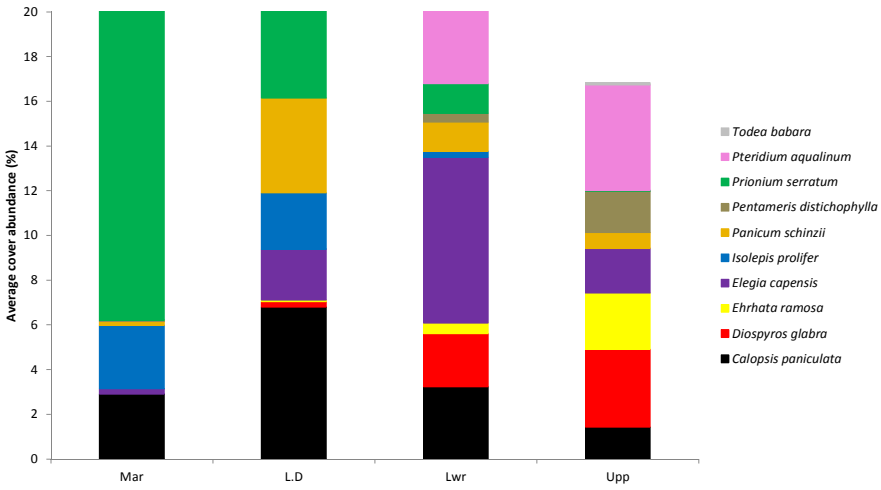

Figure 3.8 **Average abundance (% cover) of differentiating non-tree species in lateral zones. Mar = marginal, L.D. = lower dynamic, Lwr = lower, Upp = upper zone.**

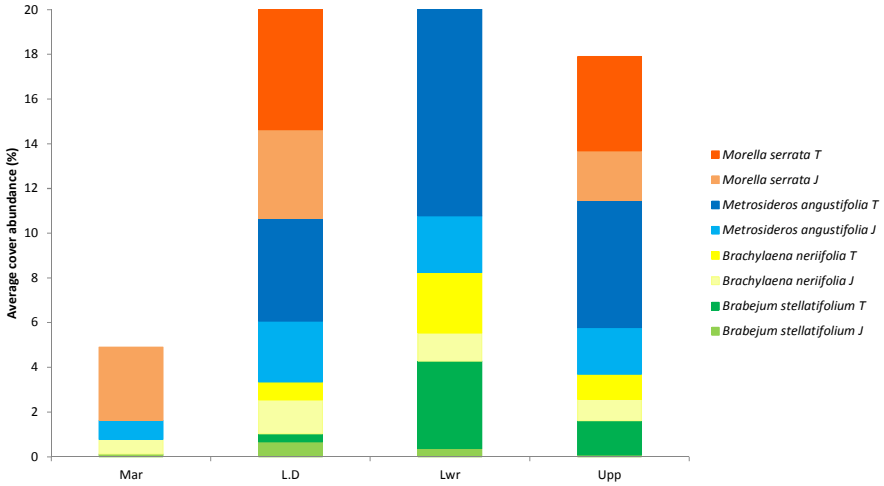

Figure 3.9 **Average abundance (% cover) of differentiating tree species in lateral zones. T = tree, J = sapling. Mar = marginal, L.D. = lower dynamic, Lwr = lower, Upp = upper zone.**

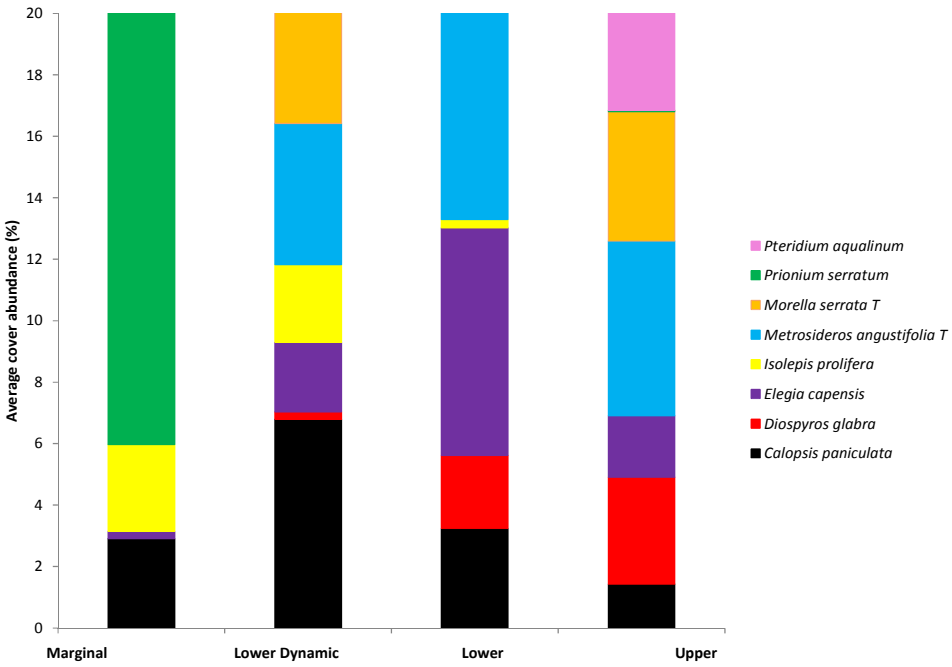

Figure 3.10 **Average abundance (% cover) of discriminating species, using a combination of tree and non-tree species, in lateral zones. T = tree. Mar = marginal, L.D. = lower dynamic, Lwr = lower, Upp = upper zone.**

3.3.3.1 Rules based on bank shape

BIOENV revealed that distance and then elevation from the water's edge (stage at dry season base flow) were the factors most strongly associated with species distributions on the river bank. The C&RT decision tree confirmed that distance and elevation were good predictors of lateral zones along with bank gradient. The primary split occurred at a horizontal distance of 1.5 m, with the marginal and lower dynamic zones being located within

that distance of the wetted channel, while the lower and upper zones were further away (Table 3.5).

Table 3.5 Physical rules for identifying lateral zones in Fynbos Riparian Vegetation. Percentage scores are the number of sample plots correctly identified by the rules during model development (observed) and the testing of predictive accuracy (test).

Bank type	Lateral zone	Physical rule	Observed	Test
Wet bank	Marginal	Distance <= 1.5 m and elevation <= 0.12 m	70%	96%
	Lower dynamic	Distance <= 1.5 m and elevation > 0.12 m	34%	26%
Dry bank	Lower	Distance > 1.5 m and elevation <= 1.29 m	86%	70%
		Distance > 1.5 m and elevation > 1.29 m and WB-DB grad > 0.23	-	-
	Upper			
Terrestrial		Distance > 1.5 m and elevation > 1.29 m and WB-DB grad <= 0.23	65%	54%

Thus, a sample plot placed within 1.5 m of the water's edge will be in either the marginal or lower dynamic zone. Of these, those positioned at elevations less than 0.12 m above the water's surface will be in the marginal zone. Those situated higher than 0.12 m will be in the lower dynamic zone. Plots located at a distance greater than 1.5 m from the water's edge will be in the lower or upper zones. Of these, those lower than 1.29 m above the water surface will be in the lower zone. Those above that height could either be in the lower or upper zones based upon the difference in gradient. Those on a convex bank (WB-DB > 0.23) will be in the lower zone, while those on a concave bank (WB-DB <=0.23) will be in the upper zone. An example of the latter case will be where the riparian area extends for some distance before the slope steepens at the adjacent terrestrial community. These rules were extremely good in predicting the location of the marginal zone and very good in predicting the location of the lower zone (*test* in Table 3.5), but less good at predicting the location of the upper zone and poor for the lower dynamic zone.

3.4 Discussion

The arrangement of four lateral zones along rivers inhabited by Fynbos Riparian Vegetation was shown to be repetitive and predictable. The fourth zone, the lower dynamic after Boucher (2002), was added to the existing naming convention of Kleynhans *et al.* (2007): the marginal, lower and upper zones. It was possible to differentiate characteristic species for the four zones and a description of these is provided in combination with rules about physical bank shape that may be used to delineate the position of the four zones along headwater streams in the Fynbos Biome.

The study rivers were chosen because they provided examples of undisturbed Fynbos Riparian Vegetation and had similar species composition. However, initial analysis of the data indicated clear river signatures driven by differences in the relative abundance of species at each of the rivers. Similar river signatures, i.e., basin-level differences in relative abundance of species rather than differences in the species themselves, has been demonstrated for aquatic macroinvertebrates, fish and riparian vegetation (Hawkins *et al.* 2000; King and Schael 2001; Roux *et al.* 2002; Wishart *et al.* 2002; Sieben *et al.* 2009) in Western Cape rivers. Here, the initial separation of sites, on the basis of river signatures, meant that the zones at each river were analysed separately, which revealed that some species were more abundant in one zone in one river and in a different zone in another. Apart from complicating the search for universal discriminating species, this highlighted the sensitivity of riparian species assemblages to subtle changes in climate and possibly flow regimes. The presence of the same species in two different lateral zones, between river basins, could have resulted from different antecedent conditions that created favourable

conditions for a species to establish in a non-characteristic zone. It may also result from phenotypic variation within one species in response to broader climatic or geological differences between river basins (Silvertown 1998; Crous *et al.* 2012). A temporal study of permanently-marked lateral zones across river basins would add insight to this as would a study of plant traits or one that transplants seedlings between river basins. Retrospectively, it seemed that the presence of signatures may also apply at a finer scale than rivers. The data presented showed that longitudinal zones within one river basin and lateral zones at a site were distinct, in terms of the combination of unique and common species abundances.

Despite compositional differences between rivers based on unique hydrogeomorphological conditions and differences in species abundances, the riparian vegetation was consistently arranged into four lateral zones. Importantly, the data showed that rules about physical bank shape can be used to delineate the position of the four zones along headwater streams of the Fynbos Biome even in the absence of detailed botanical knowledge about a site. Nonetheless this is important in South Africa, where the legislation requires on-going monitoring of the condition of the nation's river systems, but where there is currently a dearth of experienced riparian botanists. The rules provided allow for the marginal, lower and upper zones to be delineated as required by the VEGRAI assessment protocol (Kleynhans *et al.* 2007). Also, the strong links between plant distribution and elevation and distance vectors, or slope, shown across the board indicate that zone delineation can also provide a direct link to river bank hydraulics and thus to environmental flow requirements, which require an understanding of variation in the inundation of different riparian communities (Chapter 4).

Being able to delineate zones is also important in the context of the Western Cape, where many of the riparian areas are either heavily invaded by, or recently cleared of, invasive trees. Delineating zones at invaded or cleared sites will allow for a direct comparison to the species that would be expected to occur naturally and this can lead to new understanding that can assist in clearing efforts and rehabilitation of the riparian areas (see Chapter 6), as it seems likely that the indigenous species preferentially inhabiting different zones will have different life-history requirements (Francis 2006). This topic was investigated further in Chapter 5.

A fourth zone, the lower dynamic (after Boucher 2002), was added to the naming convention of Kleynhans *et al.* (2007). This new zone could not be left out as it was present to the same extent and constituted by the same levels of sample plot similarity as the other three zones. The lower dynamic zone was shown to be an area of active recruitment, as it most frequently contained the highest abundance of riparian saplings. Boucher (2002) describes this zone as a relatively open area compared with the density of riparian species in the other zones, which is characterised by regular disturbance as it is situated at the boundary between the intra-annual and inter-annual floods (see Chapter 4). On this basis, he predicted that the lower dynamic would be particularly susceptible to invasion since floods that regularly disturb this zone may mobilise sediment annually that would remove competitors and at the same time favour disturbance triggered species, such as invasives. Whether or not this prediction holds true was investigated in Chapter 6. Including this zone in assessments of riparian health can also provide information on the functioning of the riparian zone and the reproductive fitness of the adult population

The location of the four zones concurs with the descriptions of Hupp and Osterkamp (1996), Nilsson and Svedmark (2002), van Coller (1992) and Moon *et al.* (2007), who also allude to the grouping of these into two main types, *viz.*: one that is inundated intra-annually and the second inundated inter-annually. This also holds true for Boucher's (2002) wet-bank community, comprised of the marginal and the lower dynamic; and dry-bank community, comprised of the lower and upper zones. Using Boucher's division, the lower dynamic would be transitional between the wet and dry banks, while the upper would be transitional between the dry bank and the adjacent terrestrial community.

Discriminant species for each of the four zones were also described. The analysis of discriminant species took into account the variability in species' abundances between zones and that the same species was present in more than one zone. Considering the phenomenon of river signatures discussed above, it must be borne in mind that, although these indicators were shown to be characteristic of a particular zone across all the rivers, their distribution may not be restricted to that zone on any one river. Further, when comparing two rivers one or more of the indicators may be missing. This was the case between the Rondegat and the Hex Rivers that are situated in neighbouring basins, where *Erica caffra* was abundant on the Rondegat River, and is generally abundant along Fynbos rivers (Mucina and Rutherford 2006), but was not found at the four sites on the Hex River. Other species, such as *Freylinia lanceolata, Pennisetum macrourum, Salix mucronata* and *Todea barbara,* showed a similar pattern but at other rivers. The reasons for this are not known.

Trees and non-trees contributed in different ways to the patterns of zonation. Non-trees produced extremely similar patterns on their own but a combination of tree and non-tree data resulted in the highest similarity coefficients between samples groups that constituted the zones. Trees on their own did not produce a pattern that may be sensibly separated out into groups. This was probably due to their being absent from some samples, which created many outliers in the analyses. This was confounded by the fact that trees, their seedlings and their saplings, differed in their zonal specificity.

Once the zones were distinguished, it transpired that trees were fairly zone specific while saplings were less so and seedlings were non-specific. In general, there is little known about recruitment strategies of species along Fynbos rivers. The phenological study of Brown *et al.* (2004) and the seedbank study of Vosse *et al.* (2008) both consider aspects of recruitment in the context of the broader wet and dry bank communities of Boucher (2002). Wet bank occupants may be predominantly hydrochorous and disperse seed during periods of low flow in order to target the marginal and lower dynamic zone for recruitment (Nilsson and Svedmark 2002). Following this logic, it may be that hydrochorous dry bank species release seed during periods of high flow in order to disperse seeds higher up the bank to where the adults may be found. Alternately, anemochory, or wind dispersed seeds, may result in an even dispersion of seedlings across the riparian area that then only persist where conditions are favourable. Of particular relevance, given the results from temperate floodplain rivers (Mahoney and Rood 1998; Rood *et al.* 1999), was that there were no obvious groupings of successional stages, known as seres (Barbour and Billings 2002). Seres develop on floodplains as successive cohorts, or groups of individuals that are the same age, in response to favourable flood events (Naiman *et al.* 2005). The absence of seres in the headwater streams of the Western Cape rivers, combined with the non-specificity of seedlings, supports the prediction that, because of the inherent unpredictability of the hydrological flow regime, the aquatic biota of Fynbos rivers should be dominated by opportunists that lack specialist recruitment requirements (Davies and Day 1998). The findings of Galatowitsch and Richardson (2005) and Vosse *et al.* (2008), that Fynbos rivers are dominated by sprouters and not seeders, also support this. Some aspects of the phenology of *Salix mucronata, Brabejum stellatifolium* and *Metrosideros angustifolia* were investigated in Chapter 5 but this study did not overtly consider recruitment success nor the fate of seedlings that appeared to establish readily. These other aspects of recruitment form part of another study (Magoba 2013).

As a group, non-trees were more zone-specific than were trees, and when analysed alone showed the pattern of the four zones. This was possibly because the shallower roots of non-trees make them more vulnerable to the abrasive force of floods (Thorne 1990) and are thus uprooted more easily/often, which would increase the level of influence that flooding has over their bank position (Francis 2006). The shallow roots would also mean that they are sensitive to surface soil moisture, which declines with distance up the bank (Castelli *et al.* 2000). Thus, it stands to reason that plants located at different lateral positions would exhibit

different tolerances to drought, and that the transition from obligate to facultative riparian species and then to incidental or terrestrial species would be marked. If this is true then non-trees may recruit more specifically, or rely on clonal growth to persist in favourable positions. The two non-trees most strongly linked to lateral zone position were *Prionium serratum,* in the marginal zone, and *Diospyros glabra* in the upper and occasionally in the lower zones. *P. serratum* is an obligate riparian species that is dependent on surface flow and is associated with banks subject to strong scouring (Sieben and Reinecke 2008). As such, this species is not able to tolerate drying out. *P. serratum* releases seed during periods of low flow (Brown *et al.* 2003) and this would match predictions made with respect to hydrochory and preferential seed dispersal within the wetbank, although it is not known whether seeds of *P. serratum* are predominantly hydrochorous, or anemochorous, or both. *P. serratum* also reproduces clonally (Brown *et al.* 2003) and if vegetative parts of the plants are broken off during flooding these may root to establish a new individual. The ability to disperse by vegetative diaspores is a well-known characteristic of riparian pioneers (Nilsson and Svedmark 2002). No large individuals of *Diospyros glabra* were found in the wet bank although sometimes seedlings were observed here. *D. glabra* is not restricted to river environments but is in fact more common to sandy flat and dry slopes (Goldblatt and Manning 2000). Despite this, it occurred commonly in the upper zone. *D. glabra* produces red berries, a trait shared by seeds that are dispersed by animals (zoochory, Du *et al.* 2009) and seeds of this species were observed in baboon scat (personal observation). Thus, it may be that despite being an incidental species, not associated with rivers, the animals that disperse the seeds of this plant form a strong association with the river ecosystem.

A decision tree (Figure 3.11) based on a combination of the rules (Table 3.5) and indicators species (Figure 3.10) was proposed to delineate zones in Western Cape headwater streams:

- measure out a distance of 1.50 m from the dry-season wetted edge to separate the wet bank from the dry bank;
- in the wet bank, mark the vertical elevation of 0.12 m above the water's surface to separate the marginal from the lower dynamic zone;
- look for *Prionium serratum* and Isolepis prolifera in the marginal zone;
- look for *Calopsis paniculata* and *Morella serrata* in the lower dynamic zone;
- if present use their **rooted** position to adjust the boundary between the marginal and the lower dynamic zone;
- in the dry bank mark the vertical elevation of 1.29 m above the water's surface to separate the lower from the upper zone;
- look for *Calopsis paniculata* and *Morella serrata* in the lower dynamic zone;
- look for *Metrosideros angustifolia* and *Elegia capensis* in the lower zone;
- if present use their **rooted** position to adjust the boundary between the lower dynamic and the lower zone;
- look for *Metrosideros angustifolia* and *Elegia capensis* in the lower zone;
- look for *Pteridium aquilinum* and *Diospyros glabra* in the upper zone;
- if present use their **rooted** position to adjust the boundary between the lower and upper zone;
- in the upper zone, look for terrestrial plants that may be drier in texture and situated on soil that is different in colour and texture;
- use these to guide the location of the outer riparian boundary.

Overall, the similarity in the pattern across the study rivers suggests that similar zones will be present along rivers in other parts of the country, which was tested in Chapter 4. With respect to the identification of typical and differentiating species for rivers, the results obtained in this Chapter suggest that a cross-community comparison would probably produce a stronger cohort of discriminating species, so this adjustment was used in Chapter 4.

Establishing functional differences between plants that occupy different zones will lend support to the validation of the lateral zone concept by providing evidence toward a mechanistic explanation for the occurrence of lateral zones in riparian vegetation communities. This was addressed in Chapter 5.

As already suggested, the inclusion of the fourth zone, the lower dynamic, in the classification is significant partly because it represents the area of greatest recruitment of indigenous trees but also because it is the area of greatest apparent natural disturbance, and areas of disturbance are targeted by alien vegetation (Tickner *et al.* 2001). Given the magnitude of the invasion problem on Western Cape rivers, and the great trouble and expense incurred in the last decade to clear these areas (Chapter 2), recovery of Fynbos Riparian Vegetation following clearing was investigated within the framework of the zones – made possible by the decision tree – in Chapter 6 in order to establish whether or not there was any zonal differences between the mode of alien invasion and the extent of recovery of the indigenous vegetation following clearing.

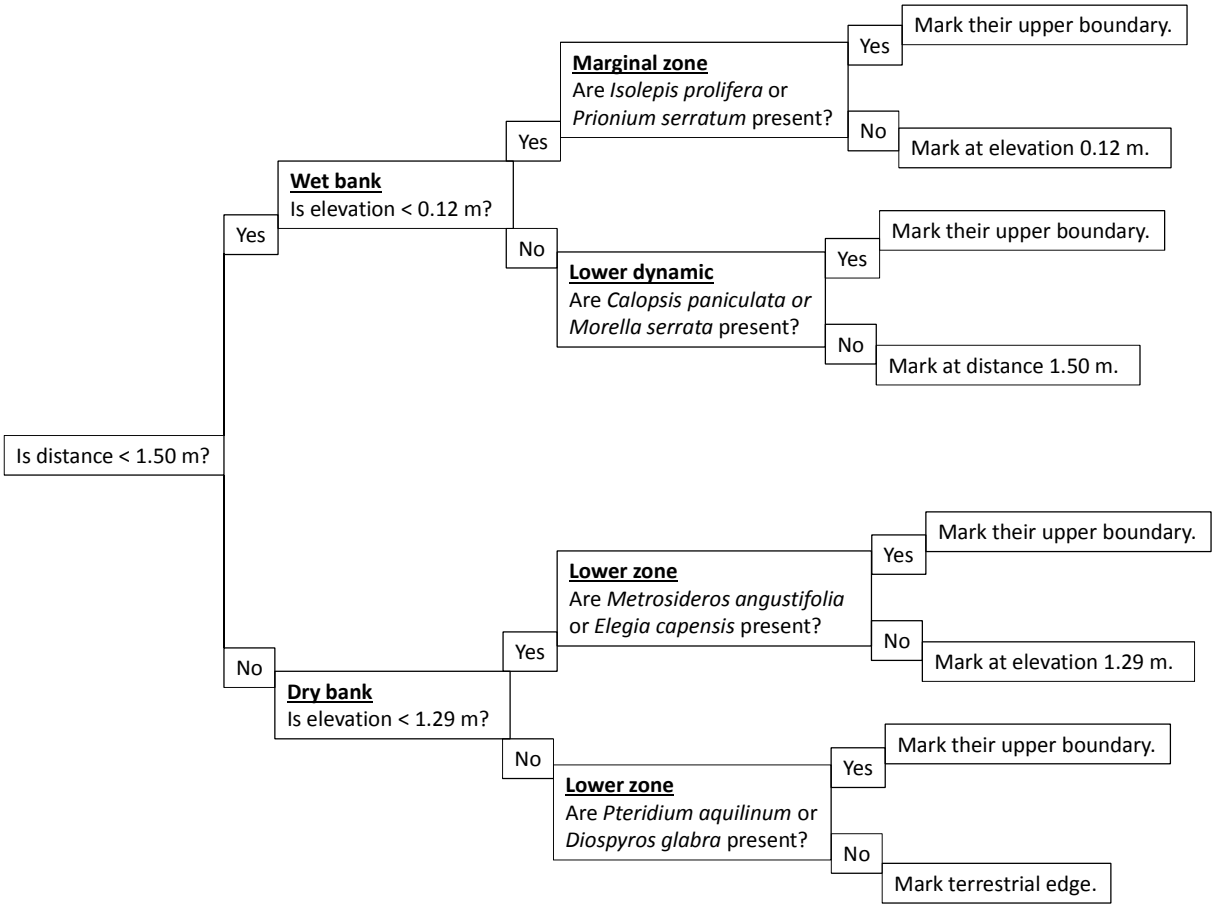

Figure 3.11 A decision tree for locating lateral zones in Fynbos Riparian Vegetation. Elevation and distance are measured from the dry-season wetted edge.

4 Links between lateral vegetation zones and river flow

This paper was presented at the South African Society for Aquatic Scientists Conference in July 2013. Karen Esler, Cate Brown and Jackie King are co-authors as each contributed towards the concepts therein and reviewed the manuscript. Martin Kidd assisted with statistical analyses and Martin Kleynhans synthesized the hydrological records and modelled the hydraulic data.

With regard to the sections listed below, the nature and scope of my contribution were as follows:

Section	Page number	Nature of contribution	Extent of contribution
4.2.3	46	Data analysis	10%
4.2.4	47	Data collection	30%
4.2.5	48	Data analysis	80%
4.3.3	59	Results from analysis	90%
8.1	117-121	Figures	0%

The following co-authors have contributed to the sections listed below:

Co-author	Email	Section	Nature of contribution	Extent of contribution
M Kleynhans	martin.kleynhans@aurecongroup.com	4.2.3	Data analysis	90%
M Kleynhans		4.2.4	Data analysis	70%
M Kidd		4.2.5	Data analysis	20%
M Kidd		4.3.3	Results of analysis	10%
M Kleynhans		8.1	Figures 8.5-8.13	100%

Signature of candidate:

Date: 23 October 2013

The undersigned hereby confirm that:

1. The declaration above accurately reflects the nature and extent of the contributions of the candidate and the co-authors in the listed sections,
2. No other authors contributed to the listed sections besides those specified above, and
3. Potential conflicts of interest have been revealed to all interested parties and that the necessary arrangements have been made to use the material in the listed sections of the dissertation.

Co-author	Signature	Institutional affiliation	Date
Martin Kidd		University of Stellenbosch	
Martin Kleynhans		Aurecongroup	

4.1 Introduction

Environmental flows describe the quantity, timing and quality off water flows required to sustain freshwater and estuarine ecosystems and the human livelihoods and well-being that depend on these ecosystems (Hirji and Davis 2009).

The assessment of environmental flows for river ecosystems is based on understanding how changes in a river's flow regime may cause changes to the biophysical conditions of the river ecosystem (Brown and King 2006) in order to quantify the volumes, quality and timing of flow required to sustain and manage the river condition at a desired state (King *et al.* 2003;

Chapter 2). Since work on environmental flows began in the 1940s two approaches to flow assessments have developed; prescriptive, in which flows are described to achieve a narrow and specific objective; and interactive, which focus on changes in river flow and one or more aspects of the river to provide a range of options for river condition (Brown and King 2006). Of the interactive approaches, two holistic methods (Arthington *et al.* 1998) are in use in South Africa, DRIFT (Downstream Response to Instream Flow Transformation, King *et al.* 2003) and the Flow Stressor-Response method (Hughes and Louw 2010). Both incorporate assessments of changes in a range of biophysical disciplines, such as hydrology, hydraulics, fluvial geomorphology, sedimentology, chemistry, botany and zoology; and socio-economic disciplines where there are subsistence users, such as sociology, anthropology, water supply, public health, livestock health and resource economics (King *et al.* 2003). For the structure and function of riparian vegetation, predicted responses to flow change are based on plant life histories including water dependency (Chapter 5), sediment transport (Lytle and Poff 2004), bank stability (Thorne 1990) and the evolution of river channel structure (Naiman *et al.* 2008).

In regions, such as South Africa, where river flow is markedly different between wet and dry seasons (Chapter 2) environmental flow assessments have tended to concentrate on the range of low flows in the wet and dry season; the magnitude, frequency and timing of intra-annual flows, which mobilise sediment within the wetted channel (Dollar and Rowntree 2003) and trigger life history events (Lytle and Poff 2004); and the frequency of occurrence of large floods, which mobilise large calibre sediments that shape the channel and inundate floodplains (Dollar and Rowntree 2003). For instance, DRIFT places an emphasis on flow variability through and between seasons in ten categories of flow (King and Brown 2006): dry season low flows, wet season low flows, four categories each of intra- and inter-annual floods of increasing magnitude and a specified number of events per year. The consequences of flow changes to riparian vegetation communities are predicted by understanding how flow influences riparian habitat and flora, for example; extreme floods reset physical river and riparian habitat (Naiman *et al.* 2008); medium floods flush riparian vegetation from the channel and small floods recharge groundwater for shallow rooted species (Naiman *et al.* 2000); normal low flows maintain the wet bank community (Boucher 2002); and drought lows enable recruitment and purge invasive riparian and aquatic species (Naiman *et al.* 2000).

Boucher (2002) linked DRIFT flow categories to lateral zones in the riparian vegetation to assess the environmental flow requirements of the Breede River, Groot Brak and Olifants-Doring (Brown *et al.* 2005); and also the Senqu (Boucher and Tlale 1998) Rivers. However, Sieben *et al.* (2009), using Boucher's (2002) lateral zone layout, found only a weak correlation with distance and elevation and alluded to hydraulic links but these were not assessed. However, the existence of these lateral zones, the fact that they can be distinguished using elevation and distance from the wetted channel (Chapter 3) points to a strong link between the position of the zones and flow events and suggests that a re-examination of this issue is warranted. Establishing such links would strengthen our ability to predict flow-related changes in riparian communities and strengthen the case toward establishing functional differences between wet and dry bank communities of Fynbos headwater streams (Chapter 5). Furthermore, it follows that if the location of lateral zones is determined by the flow regime to which the riparian community is subjected, then these zones should be evident in all kinds of rivers and the links to flow should be broadly similar across geographic areas despite climatic differences.

Based on this, I set out to determine whether the four-zone classification described in Chapter 3 applied in riparian communities in parts of South Africa with different climates and markedly different hydrographs and, if indeed they did occur, to re-examine the links between the flow regime, in particular floods, and lateral-zone position. The key questions (Figure 1.1) were, "Is the pattern of lateral zones shown for Fynbos rivers (Chapter 3) evident in riparian communities in other parts of the country?" and "Is flood recurrence interval a good

predictor for lateral zone location?" Together with the findings for Western Cape headwater streams, these were incorporated into three hypotheses:

- If lateral zones result from differential species responses to a combination of abiotic factors that vary in space and time, then the same pattern should be repeated in different biomes even though the species composition of the zones may differ. There should be two main communities: a wet bank comprising the marginal and lower dynamic lateral zones, and a dry bank comprising the lower and upper lateral zones.
- If there is a separation between the wet and dry bank communities, inundation duration should be a good predictor of the location of the wet bank community as the life histories of the plants must have evolved in response to regular inundation. The boundary between the wet and dry bank should thus be located at the upper limit of the intra-annual floods.
- If the dry bank is inundated inter-annually, it should be possible to demonstrate significant differences in flood recurrence within the ranges of these two communities along an inundation gradient.

4.2 Methods

4.2.1 Site selection

Perennial rivers were selected in three regions with distinctly different flow hydrographs (Chapter 2); summer peak flow in Mpumalanga; the aseasonal or early spring peak in the Southern Cape; and winter peak flow in the Western Cape (Joubert and Hurley 1994); and distinct riparian vegetation communities: Lowveld Riverine Forest and Northern Mistbelt Forest in Mpumalanga; Southern Afrotemperate Forest in the Southern Cape and Fynbos Riparian Vegetation in the Western Cape (Mucina and Rutherford 2006). In each area, the study focussed on laterally constrained headwater streams with predominantly longitudinal flow (Gomi *et al.* 2002) in order to minimise the complexity of the hydraulic modelling required to describe how flow may relate to bank slope (Chapter 3) and how this may correlate to plant distribution (Table 4.1).

Table 4.1 Biophysical data and location of study sites. Zonation after Rowntree *et al.* (2000). Vegetation community type from Mucina and Rutherford (2006).

Region	River (Site code)	Latitude	Longitude	Gauge	Flow record	Longitudinal zone	Vegetation Community
Western Cape (Winter high flow, summer low flow)	Molenaars (Mol1)	-33.7233	19.17179	H1H018	1969-	Upper foothills	Fynbos Riparian Vegetation
	Elands (Ela1)	-33.7392	19.1132	H1H033	1991-	Transitional	Fynbos Riparian Vegetation
	Elands (Ela2)	-33.7394	19.1131	H1H033	1991-	Transitional	Fynbos Riparian Vegetation
Southern Cape (Aseasonal flow, early spring peak)	Karatara (Kar1)	-33.8824	22.8385	K4H002	1961-	Transitional	Southern Afrotemperate Forest
	Kaaimans (Kaa1)	-33.9711	22.5478	K3H001	1961-	Transitional	Southern Afrotemperate Forest
	Diep (Die1)	-33.9136	22.7081	K4H003	1961-	Upper foothills	Southern Afrotemperate Forest
Mpumalanga (Summer high flow, winter low flow)	Crocodile (Cro1)	-25.5024	31.1820	X2H032	1968-	Lower foothills[11]	Lowveld Riverine Forest
	Mac Mac (Mac1)	-24.9999	30.8146	X3H003	1963-	Upper foothills	Northern Mistbelt Forest
	Mac Mac (Mac2)	-24.9999	30.8147	X3H003	1963-	Upper foothills	Northern Mistbelt Forest

[11] This site on the Crocodile River did not meet the geomorphological criteria but was selected as the vegetation and hydraulic criteria surpassed all other sites visited in Mpumalanga.

Least disturbed riparian areas were selected in close proximity to flow gauging weirs with reasonably accurate hydrological records in excess of 30 years The two Elands River sites in the Western Cape sites were located on the cross-sections used for the reference condition in Chapter 3 as these were the only two suited to accurate hydraulic modelling; all other sites were new.

4.2.2 Vegetation data

The method of vegetation data collection from Chapter 3 was modified in order to sample replicate vegetation transects on opposing banks in 10 m wide belt transects positioned perpendicular to the direction of flow and with the centre point (5 m) of each located along a hydraulic cross-section (Figure 4.1). Transects encompassed the channel and both macrochannel banks up to the riparian edge, which was indicated by the presence of terrestrial species at the transition between the riparian zone and the adjacent terrestrial community. Each belt transect was divided laterally into contiguous 1x5 m sample plots at all sites except Cro1, where the total length across the macrochannel exceeded 100 m. At Cro1, plots were systematically sampled every 4 m on the left bank and every 2 m on the right bank, in order to arrive at the same number of plots on each bank as at the other sites (~12). Each 1 x 5 m sample plot was surveyed along the cross-section to record its position relative to water surface elevation. Cover abundance was recorded for all species by eye (Kent and Coker 1992) and for three tree life stages: seedling (height < 0.3 m), sapling (0.3 > h > 2 m) and tree (h > 2 m).

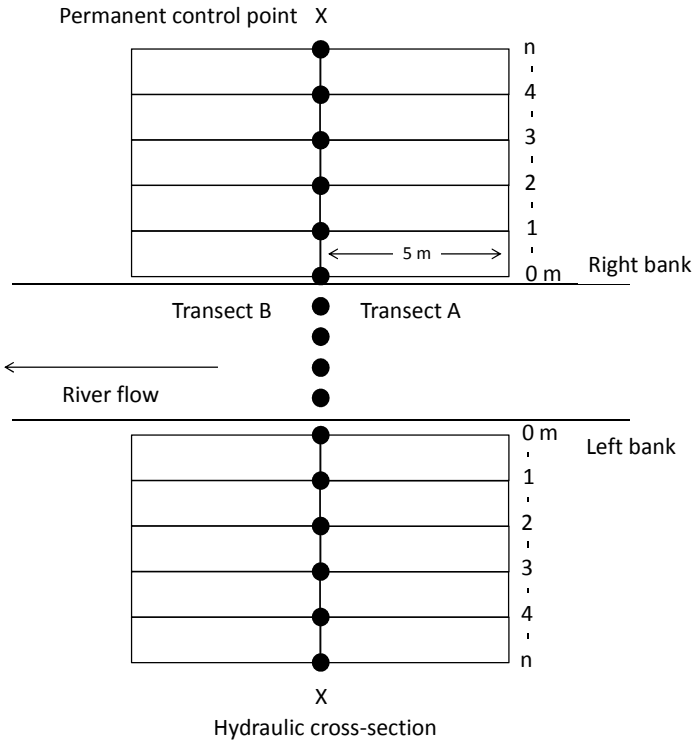

Figure 4.1 **Vegetation transects aligned adjacent to hydraulic cross-sections on both river banks. Sample plot codes (e.g. 1A = metre 1, vegetation transect A) measured from the wetted channel edge.**

The same methods of vegetation data analysis and interpretation (Chapter 3) were used to reduce the vegetation data to species abundances at a river-scale, for the purposes of comparing river basin, and at a sample-plot scale, in order to allocate lateral zones based on species habitat characteristics. The width of each zone was plotted onto the hydraulic cross-

sections and discriminating species for the lateral zones from each riparian community were tabulated.

4.2.3 Hydrological data

In order to model the occurrence of floods a time series of daily average flows was obtained from DWA (2012) for gauging stations located near each site. Data flagged as either missing or unreliable were patched for up to 20 days in length; years with larger gaps were discarded and the bounding years concatenated. Records were patched using data from nearby DWA gauges situated on the same river or a river with similar flow characteristics. Mean monthly runoff ratios between patching gauging stations were derived using common complete years with good data. These ratios were applied to observed data at the nearby station and used to infill the gaps in the target station's record. The time-series of annual maximum flood peaks obtained (DWA 2012) for each site were checked for consistency and data flagged as missing or that exceeded the gauging station rating curve were checked against the daily discharges to decide whether the peaks should be incorporated or not. Where flood peaks were missing or considered as bad data after being checked, they were ignored.

The annual maxima were then ranked and a Log Pearson III probability distribution fitted. Inter-annual flood peaks at 2, 5, 10 and 20 years were then extracted for each of the sites. Considering that all the sites had more than 20 years of good flood peak data, the estimates of the return period floods were considered to be reasonable. Daily average flow peaks were plotted on the cross-sections of each site using the rating curves produced from the hydraulic data collected along each cross-section. Four intra-annual flood classes were calculated using the DRIFT[12] guidelines (Chapter 2, Brown *et al.* 2005). The magnitude of the Class 4 intra-annual flood was calculated by subtracting 10% from the 1:2 year flood discharge. The magnitudes of the Class 3, 2 and 1 intra-annual floods were calculated as successive halves of this value.

4.2.4 Hydraulic data[13]

Water surface elevations (stage) for high and low flows were surveyed in at each cross-section. Surveys were done in September and November 2011, and March 2012 at the Western Cape sites; in November 2011, and April and June 2012 at the Southern Cape sites, and; in April, June and July 2012 at the Mpumalanga sites. A rating curve was derived for each cross-section based on the surveyed stages and discharges observed at the relevant gauging stations, which were cross checked against primary verified sub-daily data accessed from the DWA database (DWA 2012). The stage of zero flow that was surveyed in, and; one or two modelled high flows to extend the rating curve beyond the observed data. The high flows used to extend the rating curve beyond the measured points were modelled using:

- Manning's equation (Gordon *et al.* 1992) based on a single cross-section and representative high flow energy slope at Ela1, Ela2, Kaa1, Kar1, Mac1 and Mac2. Manning's n values were estimated using photographs from various references (Barnes 1967, Arcement and Schneider 1989, Hicks and Mason, 1998; Birkhead and Desai, 2009) and personal experience (Mr Martin Kleynhans, Aurecon Group, Cape Town, South Africa). In addition, the variation of Manning's resistance[14] with stage was determined by plotting the Manning's resistances back-calculated from the observed

[12] The DRIFT (Downstream Response to Imposed Flow Transformation) methodology is an interactive scenario based method for calculating river ecosystem responses to manipulated flow regimes. Needs a reference

[13] Modelling of hydrological and hydraulic data was completed by Mr Martin Kleynhans of Aurecon Group, Cape Town, South Africa, a co-author on this paper.

[14] Manning resistance (*n*): is a composite factor that accounts for the effects of many forms of flow resistance. In general, *n* increases as turbulence and flow retardance effects increase (Gordon *et al.* 1992).

stages, discharges and slopes. The energy slope was measured off a 1:50 000 scale topographical map with 20 m contours or was surveyed off the channel bed over a reasonable distance *ca.* 100 m.

- A one-dimensional hydraulic model (HEC-RAS) consisting of at least three cross-sections and a downstream boundary condition consisting of:
- a surveyed downstream normal depth (slope) at Mol1.
- a known rating curve for Die1 (DWA 2012).
- The existing cross-section and rating curve (Birkhead and Desai 2009) derived for the EWR study (DWA 2010) at Cro1 – since the original cross-section was re-surveyed from the existing benchmarks and had not changed since the Reserve study.
- The rating curve was determined by fitting equation 1 to the rating points:

$$y = aQ^b + c \qquad \text{Equation 1}^{15}$$

Each time-series of daily average flows was translated to a time-series of stage via the rating curve in order to generate an (1) annual and (2) monthly time-series of daily averaged inundation durations and standard deviations about these means at 0.1 m intervals along the hydraulic cross-sections. These statistics were generated for the median year, in terms of mean annual runoff for the most recent years since a significant disturbance event, the timing of which varied per river. The rivers in Mpumulanga experienced catastrophic flooding in February 2000 and so the hydrological years from October 2000 to September 2011 were used. The rivers in the Southern Cape experienced large floods in November 2007 and so the hydrological years from October 2008 to September 2011 were used. The rivers in the Western Cape experienced a large flood in June 1996 so the most recent 11 years available were used, from October 2000 to September 2011.

4.2.5 Relating plant distribution to hydraulic variables

The position of the eight flood classes and the lateral zones on the hydraulic cross-sections were compared graphically (Appendix Figure 8.5 - Figure 8.13). The distribution of plants along each hydraulic cross-section was related to elevation, distance, flow exceedance probability, number of days inundated during a year (inundation duration) and the standard deviation about the inundation period using the BEST routine in PRIMER (V6, Clarke and Warwick 2006), a correlation technique that links multivariate biological patterns with multiple environmental variables. The recurrence interval (the inverse of the exceedance probability at a particular bank position) and inundation duration associated with the mid-point of each lateral zone at all sites were tabulated. The relationship between exceedance probability and inundation duration was tested using a range of univariate statistics in STATISTICA (V12, StaSoft 2013). Since each vegetation transect comprised a different number of sample plots with different lengths it was necessary to use a sub-sample. Five distance groups were assigned systematically along the vegetation transects to overcome the bias of more sample plots being present in each lateral zone along longer versus shorter transects. At each point a sample plot was selected along the hydraulic cross-sections and Least Squares Differential (LSD) tests were used to test the significance of the relationship between the lateral zone assigned to this sample plot, the probability that it was inundated (exceedance probability) and the duration of inundation.

[15] Where: (y) is stage, (Q) is discharge and (a), (b) and (c) are constants. (c) Denotes the depth of zero discharge and thus is often zero in riffles where zero discharge occurs at zero depth.

4.3 Results

4.3.1 River basin comparisons

Replicate samples from each site grouped together according to riparian community (Figure 4.2) and within this according to river. Where there were two sites at a river, the replicates on each bank grouped together.

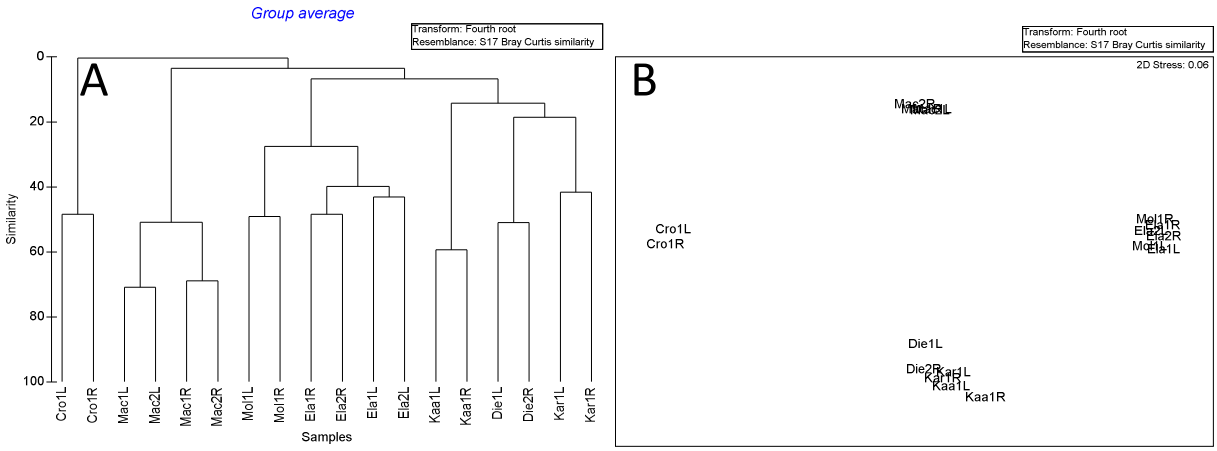

Figure 4.2 (A) CLUSTER and (B) MDS ordination of Bray Curtis similarity between species composition of sites. Site codes as per Table 4.1. L= left bank, R = right bank.

4.3.2 Patterns of lateral zonation

4.3.2.1 Fynbos Riparian Vegetation in the Western Cape

The marginal, lower dynamic, lower and upper zones were present at five of the six Fynbos sites (Figure 4.3 -Figure 4.5): on both banks of Mol1 and Ela1 and on the left bank of Ela2. There was no marginal zone on the right bank of Ela2, a pool site. There were, however, marginal-zone species scattered along the steep wetted channel edge, which comprised large cobbles and boulders that were mostly not suited to colonising graminoids, the fine rooted plants that constitute a large proportion of the marginal-zone flora (Table 4.2).

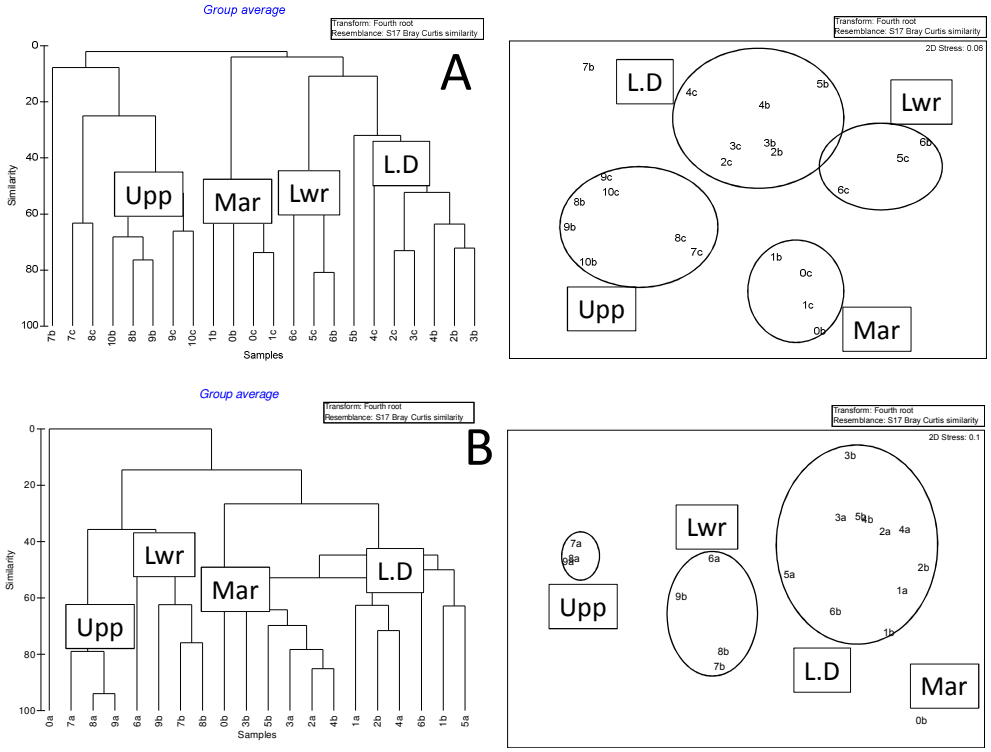

Figure 4.3 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on (A) the left and (B) right banks at Mol1. Mar = marginal, L.D. = lower dynamic, Lwr = lower and Upp = upper. Sample plot codes as per Figure 4.1.**

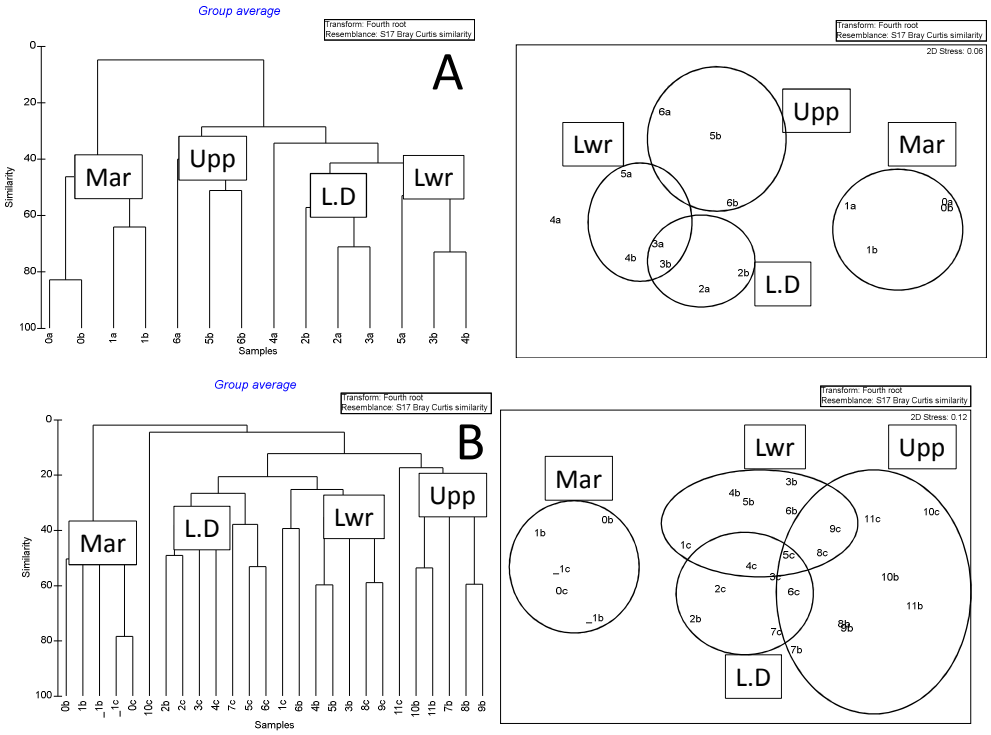

Figure 4.4 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on (A) the left and (B) right bank at Ela1. Mar = marginal, L.D. = lower dynamic, Lwr = lower and Upp = upper. Sample plot codes as per Figure 4.1.**

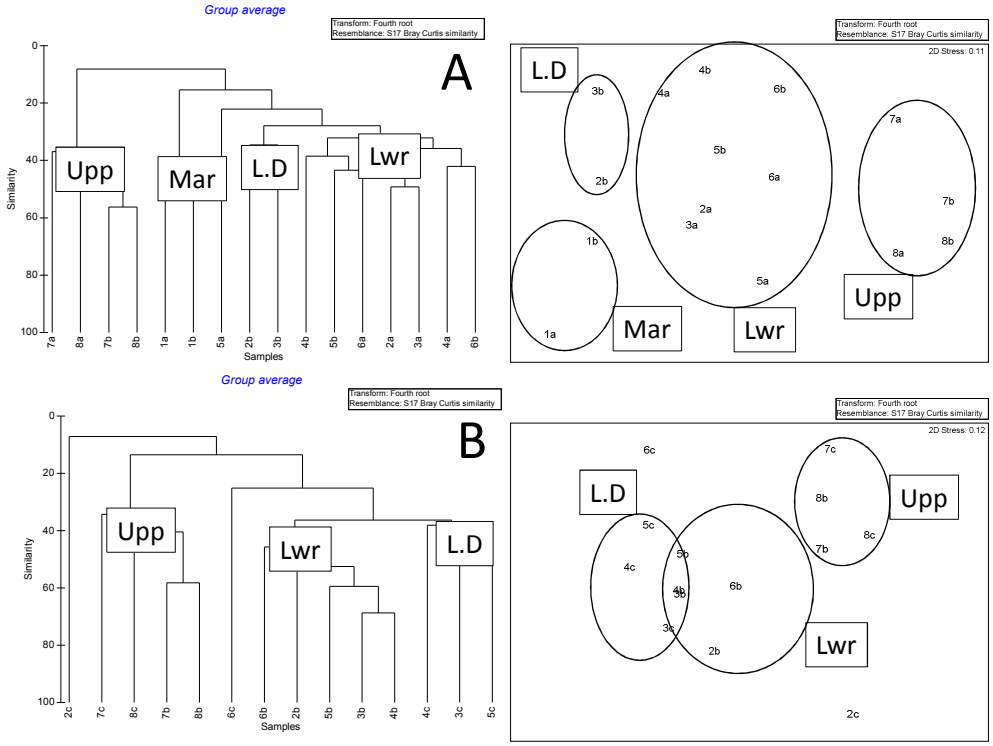

Figure 4.5 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on (A) the left and (B) right bank at Ela2. Mar = marginal, L.D. = lower dynamic, Lwr = lower and Upp = upper. Sample plot codes as per Figure 4.1.**

4.3.2.2 Southern Afrotemperate Forest in the Southern Cape

There was no marginal zone on either bank at Kar1 where the dry-season wetted channel edge was bedrock controlled and consisted of large boulders and cobbles (Figure 4.6). The marginal, lower dynamic, lower and upper zones were present on both banks of Kaa1 (Figure 4.7) and Die1 (Figure 4.8).

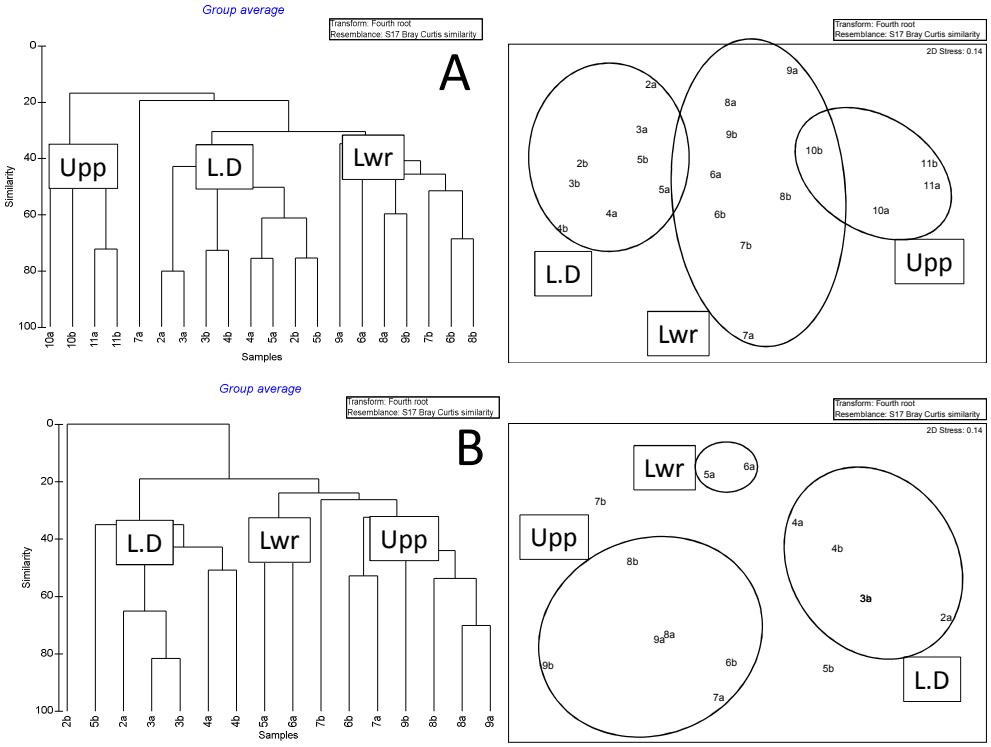

Figure 4.6 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on (A) the left and (B) right bank at Kar1. Mar = marginal, L.D. = lower dynamic, Lwr = lower and Upp = upper. Sample plot codes as per Figure 4.1.**

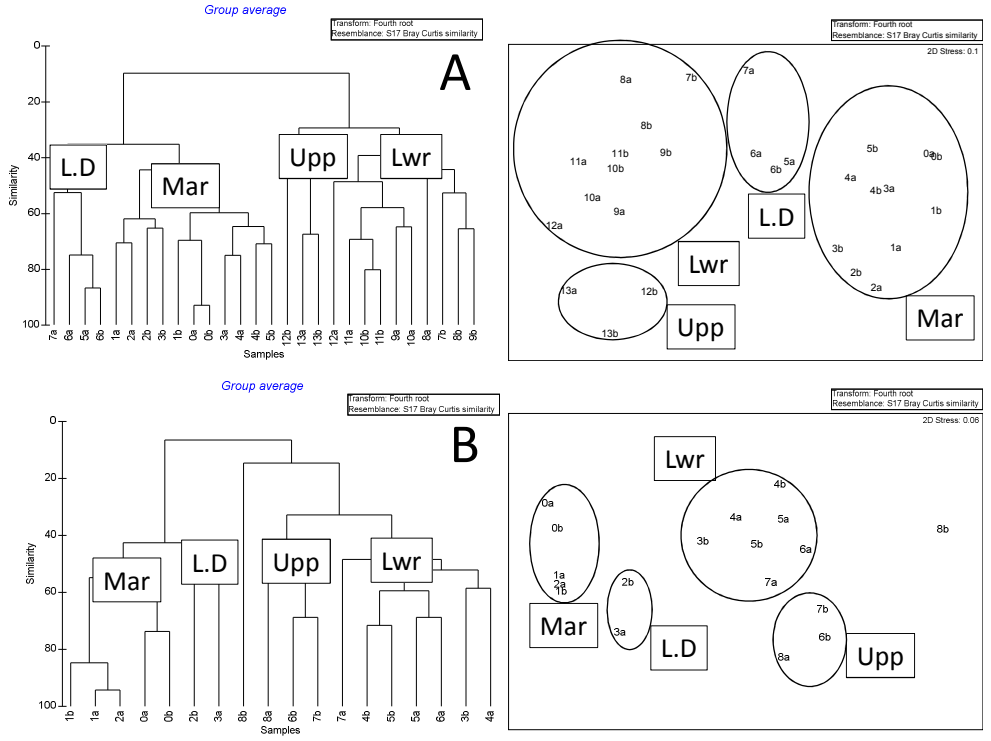

Figure 4.7 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on (A) the left and (B) right bank at Kaa1. Mar = marginal, L.D. = lower dynamic, Lwr = lower and Upp = upper. Sample plot codes as per Figure 4.1.**

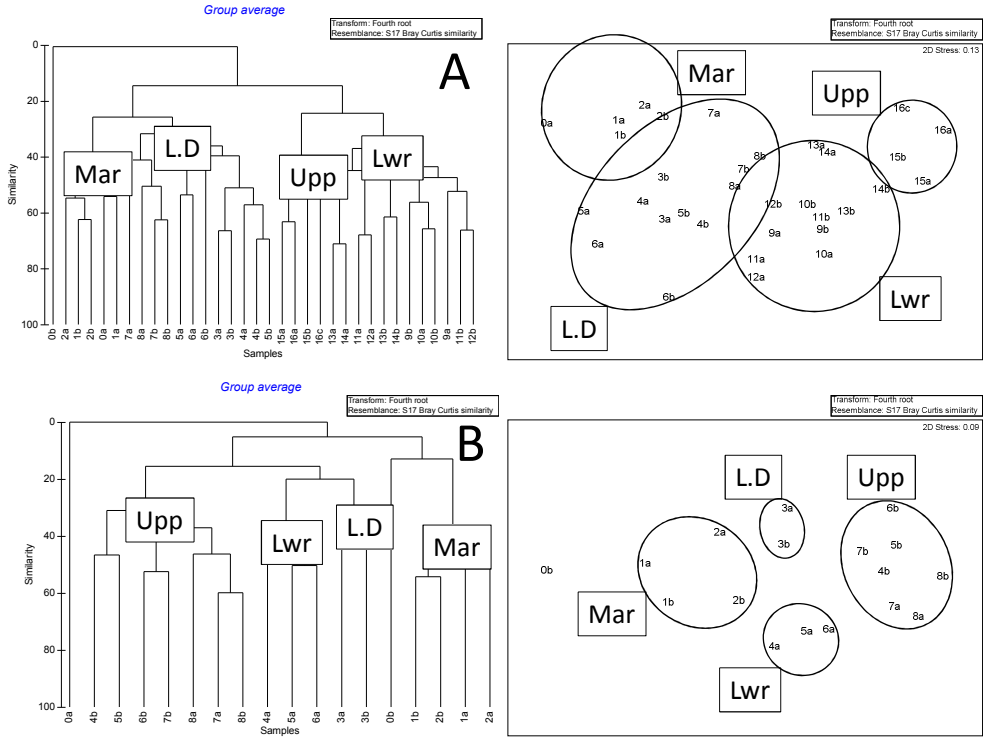

Figure 4.8 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on (A) the left and (B) right bank at Die1. Mar = marginal, L.D. = lower dynamic, Lwr = lower and Upp = upper. Sample plot codes as per Figure 4.1.**

4.3.2.3 Lowveld Riverine Forest and Northern Mistbelt Forest in Mpumalanga

The marginal, lower dynamic, lower and upper zones were present on both banks at Cro1 (Figure 4.9). There was no marginal zone at Mac1 (Figure 4.10) or Mac 2 (Figure 4.11) where the dry-season wetted channel edge was steep and comprised large cobbles and boulders unsuitable for the establishment of graminoids. The lower zone was also missing from the left bank at Mac1, which was near vertical. Here, there was only a lower dynamic zone at the water's edge and an upper zone located at the cliff ledge and beyond.

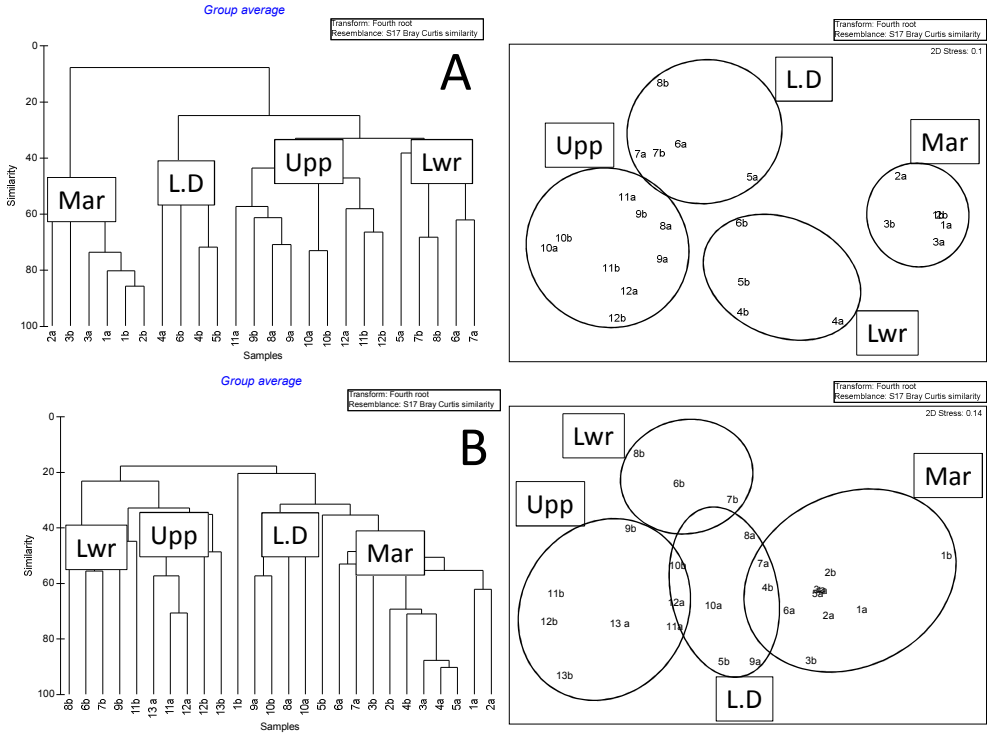

Figure 4.9 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on (A) the left and (B) right bank at Cro1. Mar = marginal, L.D. = lower dynamic, Lwr = lower and Upp = upper. Sample plot codes as per Figure 4.1.**

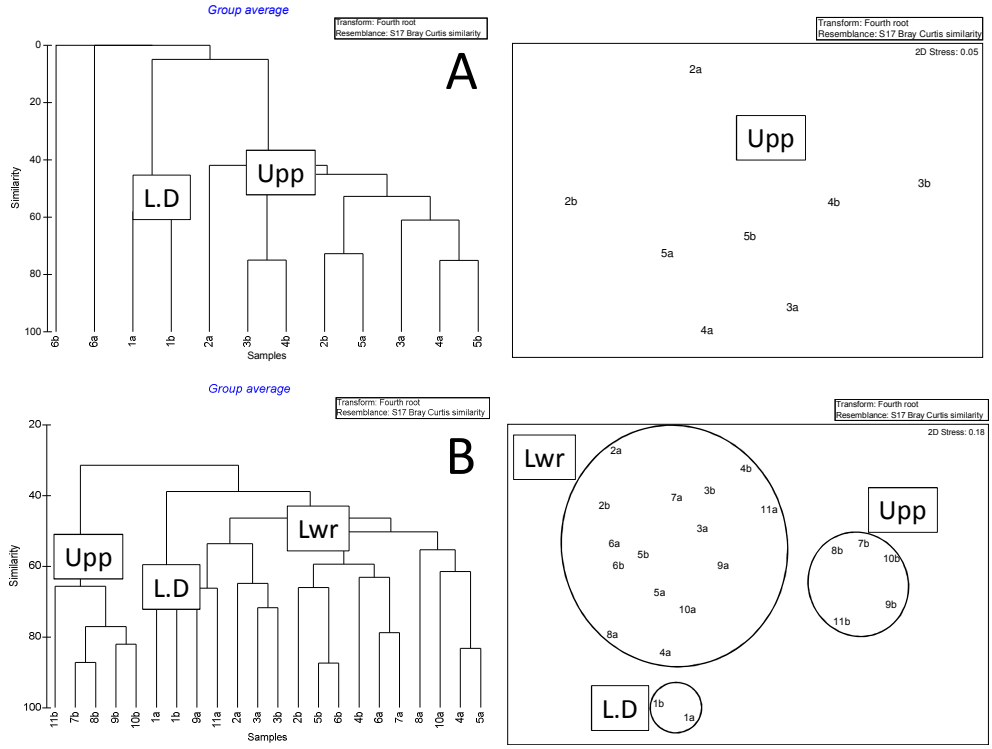

Figure 4.10 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on (A) the left and (B) right bank at Mac1. Mar = marginal, L.D. = lower dynamic, Lwr = lower and Upp = upper. Sample plot codes as per Figure 4.1.**

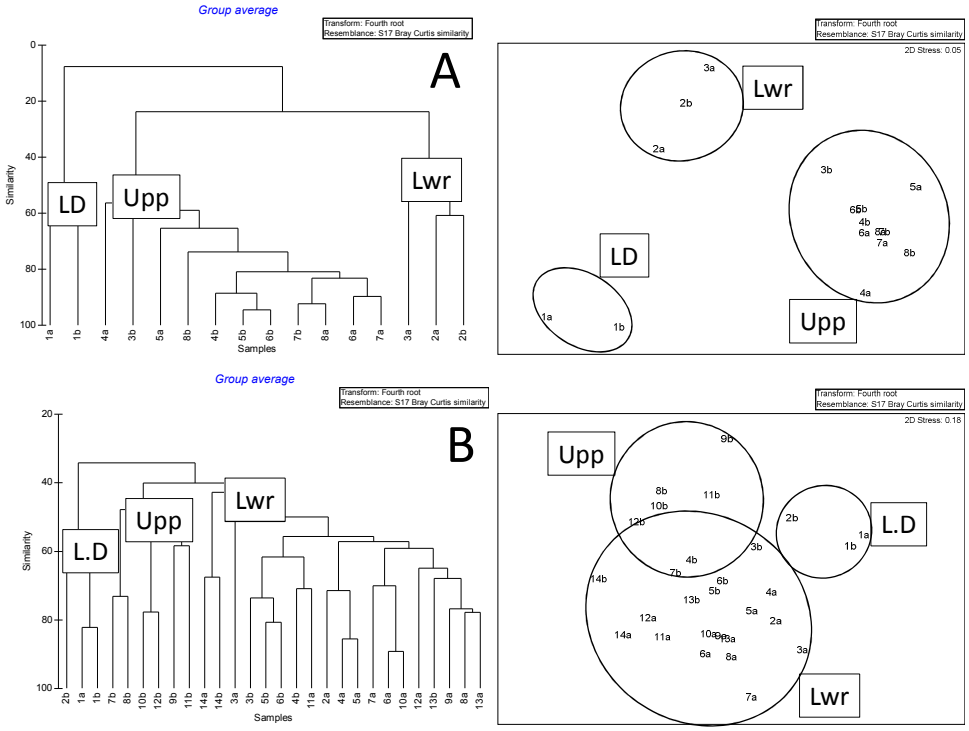

Figure 4.11 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots on (A) the left and (B) right bank at Mac2. Mar = marginal, L.D. = lower dynamic, Lwr = lower and Upp = upper. Sample plot codes as per Figure 4.1.**

4.3.2.4 Differentiating species for each lateral zone

The marginal zone was distinguished by graminoids (sedges, rushes, reeds and grasses, Table 4.2) and rhizomatous perennials; mostly ferns but also palmiet, *Prionium serratum*, in the Fynbos and Southern Afrotemperate communities. These coexisted with the Cape willow (*Salix mucronata*) on the Fynbos rivers, and the Matumi (*Breonadia salicina*) on the Lowveld Forest river. There was no marginal zone recorded at the Mistbelt Forest river.

The lower dynamic zone at the Fynbos rivers was distinguished by the common restio *Calopsis paniculata* that coexisted with the river heath *Erica caffra*. At the Southern Afrotemperate rivers the rhizomatous perennials *Todea barbara* and *Dietes iridioides* distinguished the lower dynamic zone. *Panicum maximum* distinguished the lower dynamic of the Lowveld Forest river, and *Searsia batophylla,* along with a mixture of rhizomatous perennials and sedges, distinguished the lower dynamic at the Mistbelt Forest river.

The lower zone of the Fynbos rivers was distinguished by the tree *Brachylaena neriifolia* and the restio *Elegia capensis.* The Southern Afrotemperate river lower zones were distinguished by the grass *Ehrharta rehmannii* and the rhizomatous perennial *Aristea ensifolia.* The lower zones on the Lowveld Forest river were distinguished by the tree *Bridelia cathartica* and the shrub *Phyllanthus reticulatus.* The Mistbelt Forest river lower zones were discriminated by the rhizomatous perennial *Chelianthes viridis* and the shrub *Leucosidea sericea*.

Table 4.2 **Differentiating species for each zone type in each community. Mar = marginal, L.D = lower dynamic, Lwr = lower and Upp = upper.**

Community	Site	Mar	L.D	Lwr	Upp	Growth form	Flow dependency
Fynbos Riparian Vegetation	*Juncus lomatophyllus*	■				Sedge	Obligate
	Isolepis prolifera	■				Sedge	Obligate
	Prionium serratum	■				Rhizomatous perennial	Obligate
	Salix mucronata	■				Tree	Obligate
	Erica caffra		■			Shrub	Facultative
	Calopsis paniculata		■			Restiod	Obligate
	Metrosideros angustifolia		■	■		Tree	Facultative
	Brachylaena neriifolia			■		Tree	Facultative
	Elegia capensis			■		Restiod	Obligate
	Searsia angustifolia			■	■	Shrub	Incidental
	Diospyros glabra			■	■	Shrub	Incidental
	Restio perplexus				■	Restiod	Incidental
	Pteridium aquilinum				■	Rhizomatous perennial	Incidental
	Tribolium uniolae				■	Grass	Incidental
	Erica pinea				■	Shrub	Incidental
Southern Afrotemperate Forest	*Juncus lomatophyllus*	■				Sedge	Obligate
	Juncus effusus	■				Sedge	Obligate
	Prionium serratum	■				Rhizomatous perennial	Obligate
	Calopsis paniculata		■			Restiod	Obligate
	Hippia frutescens		■			Shrub	Facultative
	Todea barbara		■			Rhizomatous perennial	Obligate
	Dietes iridioides		■			Rhizomatous perennial	Incidental
	Ehrharta rehmannii			■		Grass	Incidental
	Aristea ensifolia			■		Rhizomatous perennial	Incidental
	Blechnum punctulatum				■	Rhizomatous perennial	Incidental
	Histiopteris incisa				■	Rhizomatous perennial	Incidental
	Searsia chirendensis				■	Tree	Incidental
	Canthium ventosum				■	Tree	Incidental
Lowveld Riverine Forest	*Cynodon dactylon*	■				Grass	Facultative
	Phragmites mauritianus	■				Reed	Obligate
	Breonadia salicina	■				Tree	Obligate
	Conyza scabrida	■	■			Shrub	Facultative
	Panicum maximum		■			Grass	Obligate
	Ischaemum fasciculatum		■	■		Grass	Facultative

Community	Site	Mar	L.D	Lwr	Upp	Growth form	Flow dependency
	Bridelia cathartica					Tree	Facultative
	Phyllanthus reticulatus					Shrub	Facultative
	Gymnosporia senagalensis					Tree	Incidental
	Tagetes minuta					Shrub	Incidental
	Baleria elegans					Shrub	Incidental
Northern Mistbelt Forest	*Lunularia sp.*					Rhizomatous perennial	Obligate
	Searsia batophylla					Tree	Obligate
	Juncus effusus					Sedge	Obligate
	Cliffortia linearifolia					Shrub	Incidental
	Carex spicata					Sedge	Facultative
	Cyathea capensis					Rhizomatous perennial	Facultative
	Chelianthes viridis					Rhizomatous perennial	Facultative
	Ehrharta sp.					Grass	Incidental
	Leucosidea sericea					Shrub	Facultative
	Setaria megaphylla					Grass	Facultative
	Buddleja salvifolia					Tree	Facultative
	Pteridium aquilinum					Rhizomatous perennial	Incidental

Terrestrial species from the neighbouring community adjacent to each site distinguished the upper zones and these are likely to differ between conspecific riparian communities for reasons that have nothing to do with river flow so they were excluded from this study. The mere presence of terrestrial species in these headwater streams distinguished the upper zone from the lower zone and indicated the outer boundary of the riparian area.

4.3.3 Hydraulics of lateral zones

The distribution of plants correlated fairly well with the two main hydraulic variables: inundation duration and exceedance probability (Table 4.3), with R^2 values for both factors ranging between 0.4 and 0.7. Approximately one fifth of the sites were weakly correlated to one or both of these variables with R^2 values < 0.4, while approximately one sixth had strong relationships, R^2 > 0.7. The strongest correlation coefficients (BEST, PRIMER V6, Clarke and Warwick 2006) were described for a combined set of variables at all sites except for Kar1 that related to elevation alone and Mac1 that related to inundation duration alone. Ten of the combined relationships were strong, six were fair and two were weak and included distance and elevation vectors as well as the standard deviation about the mean inundation period.

Table 4.3 Correlations between plant distribution and inundation duration (I-D), standard deviation about this mean (δI-D) and probability of being inundated (Ex.P). LB = left, RB = right bank. BEST factors are environmental variables with the strongest correlations coefficients. Site codes as per

Community	Site	R^2	BEST Factors	I-D	Ex.P
Fynbos Riparian Vegetation	Mol1 LB	0.537 (1%)	Distance, δI-D	0.398	0.296
	Mol1 RB	0.631 (1%)	Distance, Ex.P	0.566	0.525
	Ela1 LB	0.825 (1%)	I-D, δI-D	0.716	0.440
	Ela1 RB	0.639 (1%)	Distance, elevation, δI-D	0.458	0.394
	Ela2 LB	0.707 (1%)	Elevation, Ex.P, I-D	0.428	0.529
	Ela2 RB	0.612 (1%)	Distance, elevation, Ex.P, δI-D	0.402	0.399
Southern Afrotemperate Forest	Kar1 LB	0.698 (1%)	Elevation	0.443	0.270
	Kar1 RB	0.582 (1%)	Distance, Ex.P	0.536	-0.090
	Kaa1 LB	0.846 (1%)	Distance, Ex.P	0.443	0.816
	Kaa1 RB	0.784 (1%)	Distance, Ex.P	0.642	0.737
	Die1 LB	0.777 (1%)	Distance, elevation, I-D, δI-D	0.499	0.623
	Die1 RB	0.733 (1%)	Distance, elevation, I-D	0.662	0.716
Lowveld Riverine Forest	Cro1 LB	0.793 (1%)	Distance, Ex.P, δI-D	0.677	0.748
	Cro1 RB	0.609 (1%)	Distance, elevation, Ex.P	0.208	0.503
Northern Mistbelt Forest	Mac1 LB	0.887 (1%)	I-D	0.887	0.830
	Mac1 RB	0.383 (1%)	Distance, I-D	0.293	0.298
	Mac2 LB	0.870 (1%)	Ex.P	0.660	0.870
	Mac2 RB	0.369 (2%)	I-D	0.369	0.262

Inundation duration of the marginal zone ranged from 19 to 234 days a year about a mean value of 110 ± 21 days, every 1.0 years on average (Table 4.4). The lower dynamic zone was inundated between 0.7 and 109 days a year about an average of 24 ± 11 days, every 1.9 years on average. The lower zone was inundated between 0.1 and 10 days a year about an average of 2 ± 1 days, every 15.3 years on average. The upper zone was inundated between 0.1 and 3 days a year about an average of 0.3 ± 0.2 days, every 66.3 years on average.

Tests of the relationship between inundation duration, exceedance probability and lateral zone type (Table 4.5) showed that the ranges of exceedance for the marginal and lower dynamic zones overlapped. This was because the lower dynamic zone was situated at the edge of the dry-season wetted channel if the marginal zone was absent. The marginal zone was inundated every 1.1 - 1.6 years, while the lower zone was inundated every 1.3 - 1.6

years. Since both these inundation patterns recur intra-annually it was not possible to separate them using the stage of different flood events on a cross-section. It was however possible to separate them using the duration of inundation since the marginal was inundated for longer (12 to152 days each year), compared with the lower dynamic (8 to 12 days a year).

Table 4.4 **Average number of days inundated annually (I-D ± Standard Deviation) and recurrence intervals (RI, years) associated with lateral zones. Site codes as per Table 4.1. LB = left, RB = right bank. Mar = marginal, L.D = lower dynamic, Lwr = lower, Upp = upper.**

Community	Site	Mar		L.D		Lwr		Upp	
		I-D	RI	I-D	RI	I-D	RI	I-D	RI
Fynbos Riparian Vegetation	Mol1 LB	216 ± 23	<1	42 ± 14	<1	10 ± 5	1.0	3 ± 2	1.1
	Mol1 RB	216 ± 23	<1	35 ± 13	<1	3 ± 2	1.1	0.3 ± 0.4	3.5
	Ela1 LB	225 ± 20	<1	37 ± 10	<1	<0.1	8.5	<0.1	72.7
	Ela1 RB	173 ± 6	<1	11 ± 5	1.0	0.1 ± 0.3	5.5	<0.1	>100
	Ela2 LB	234 ± 20	<1	109 ± 19	<1	15 ± 6	<1	<0.1	2
	Ela2 RB	-	-	28 ± 9	<1	1 ± 0.9	1.5	<0.1	33
Southern Afrotemperate Forest	Kar1 LB	-	-	9 ± 8	1.0	0.3 ± 0.5	12.9	<0.1	>100
	Kar1 RB	-	-	12 ± 9	1.0	1 ± 0.8	2.9	<0.1	>100
	Kaa1 LB	22 ± 22	1.0	4 ± 4	1.3	<0.1	>100	<0.1	>100
	Kaa1 RB	36 ± 34	1.0	13 ± 13	1.0	2 ± 2	1.8	<0.1	>100
	Die1 LB	42 ± 40	1.0	0.7 ± 0.9	3.3	<0.1	20.1	<0.1	>100
	Die1 RB	19 ± 20	1.1	0.7 ± 0.6	2.8	<0.1	15.0	<0.1	66.0
Lowveld Riverine Forest	Cro1 LB	18 ± 13	1.0	0.8 ± 1	3.1	0.3 ± 0.7	4.2	<0.1	>100
	Cro1 RB	18 ± 13	1.0	6 ± 7	1.7	<0.1	8.7	<0.1	47.3
Northern Mistbelt Forest	Mac1 LB	-	-	5 ± 6	3.4	-	-	<0.1	>100
	Mac1 RB	-	-	108 ± 66	1.0	<0.1	22.3	<0.1	27.9
	Mac2 LB	-	-	4 ± 1	6.6	0.1 ± 0.0	32.4	<0.1	84.0
	Mac2 RB	-	-	12 ± 5	3.7	0.2 ± 0.0	21.3	<0.1	55.8
AVERAGE		110 ± 21	1.0	24 ± 11	1.9	2 ± 1	15.3	0.3 ± 0.2	66.3

Table 4.5 **Relationships between lateral zones and exceedance probability and inundation duration. Asterisked values are significant at the 5% level. Distance groups are systematic distances along vegetation transects. Lateral zones Mar = marginal, L.D. = lower dynamic, Lwr = lower, Upp = upper. Exceedance probability is that of being inundated once annually.**

Distance Group	Lateral zone	Exceedance Probability	Inundation duration (days)	Recurrence interval (years)
1	Mar	0.92 ± 0.04*	152.3 ± 21.5*	1.1*
1	L.D	0.75 ± 0.05*	8.5 ± 28.9*	1.3*
2	Mar, L.D	0.62 ± 0.08*	11.9 ± 3.7*	1.6*
3	Lwr, Upp	0.41 ± 0.08*	4.4 ± 3.3*	2.4*
4	Upp	0.19 ± 0.06	0.7 ± 0.3	5.3

Further, if the standard deviation about these inundation periods is taken into account, a major difference emerges as the marginal zone is inundated every year while the lower dynamic is not inundated in drier years, since the variance about inundation of the lower limit of the lower dynamic is greater than the mean value. This is an important distinguishing feature and may help to explain the transitional nature of the plants that occupy this zone, which is a transitional zone between marginal and lower zone species. The boundary between the lower dynamic zone and the two higher zones is at the position of the 1:2 year flood on a cross-section.

The marginal and lower dynamic zones collectively form the wet bank and the lower and upper zones collectively form the dry bank and thus a wet bank/dry bank separation occurs at the point where the 1:2 flood recurs. The lower and upper zones were separable from the wet bank hydraulically but not from one another since their distributions overlapped; the lower zone and the lower limit of the upper zone were inundated for 1-7 days every 2.4 years. There was no relationship between the upper zone and these variables.

4.4 Discussion

Species comparisons between rivers showed that rivers grouped into the four biogeographic regions and thereafter displayed the river signatures described in Chapter 3. At a site-scale, the four lateral zones were evident on every river and were correlated with the timing, duration and magnitude of small to medium flood events and low flows.

The four zones described for Fynbos Riparian Vegetation (Chapter 3) were evident at all of the other rivers tested despite major differences in geographic location, vegetation community type, climate and patterns of seasonal flow. This concurs with studies from elsewhere in the world that report on two wet bank zones inundated intra-annually and two dry bank zones inundated inter-annually (Harris 1988; Hupp and Osterkamp 2002; Nillson and Svedmark 2002), and those in southern Africa (Hughes 1990; Boucher 2002; Kleynhans *et al.* 2007) that propose a separation between lateral zones at the boundary of the annual or channel-forming flood (Gordon *et al.* 1992). At one site, a near vertical cliff separated the lower dynamic from the upper zone, while at some others, where the wetted channel edge was comprised of large calibre sediment such as boulders, the marginal zone was missing. In some cases, this was attributed to the absence of specialist riparian trees with pioneering attributes (Rood *et al.* 2005), such as *Salix mucronata* and *Breonadia salicinia,* that are able to root on larger calibre sediments (van Coller *et al.* 1997), but where these trees were absent, it was attributed to the inability of finely rooted water-logged graminoids (Koncalova 1990), such as rushes, sedges and reeds that often make up the marginal zone, to establish. In all cases, plants that would constitute the missing zone were observed to occur upstream or downstream and so the reason for their absence was actually due to the narrow transect width chosen for the hydraulic modelling.

The geographical variation in species making up the lateral zones tends to mask the functional links driving the location of the zones. To reduce the noise within the data set, the species in each zone were categorised according to their known flow dependence, viz.: obligate, facultative or incidental riparian species (as per Chapter 3). Grouping species into these water-dependent categories showed that despite species differences, the functional distribution between zones was the same across all the sites regardless of geographic location (Figure 4.12). In general, adults of obligate riparian species occurred in the marginal zone, those of facultative species in the lower zone and those of incidental species in the upper zone. Incidental species recruited into the upper zone but rarely grew to adulthood probably because they were unable to cope with regular inundation. Recruitment of obligate species was generally restricted to the wet bank while that of facultative species was more widely distributed in the wet and dry banks (Chapter 3). This distribution of functional types supports arguments for an Ecohydrological basis for niche separation along a hydraulic gradient (Francis 2006). This has been demonstrated experimentally by Silvertown *et al.* (2009) and Araya *et al.* (2010) in seasonally wetted Fynbos communities and is investigated further in Chapter 5. Categorising responses into functional types also supports the proposition by Merrit *et al.* (2010) to move away from species-level indicators for studies on environmental water requirements in favour of categories according to flow-linked life history traits. Certainly, the results obtained in this study suggest that riparian vegetation communities respond to the flow regime in a consistent manner, regardless of geographic or climatic variation and/or species composition.

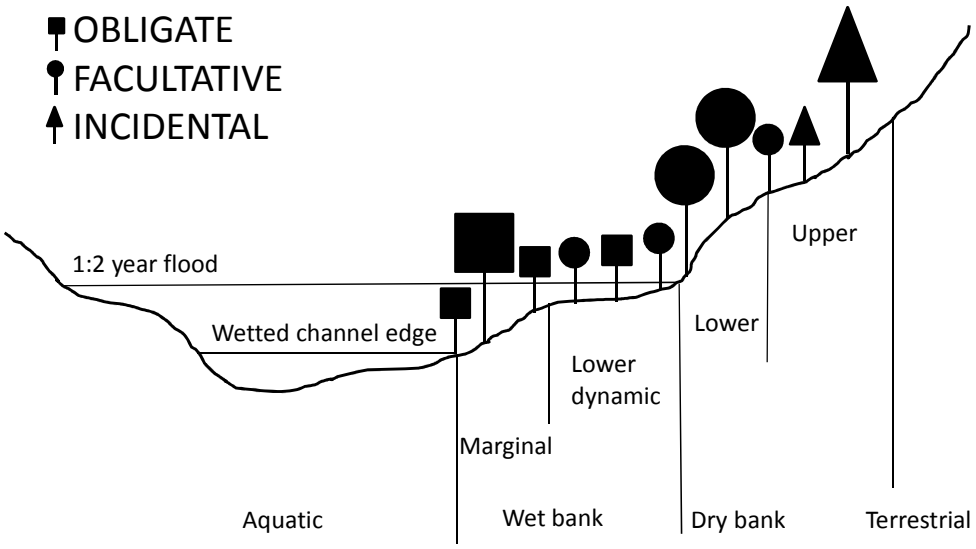

Figure 4.12 Schematic of lateral zone distribution in relation to river flow. Big symbols are adults, small are saplings.

The four lateral zones separated out based on a combination of flood recurrence and inundation duration. The wet bank was separated from the dry bank at the position on the channel cross-section, where the 1:2 year flood stage was found, and the two wet bank zones, the marginal and the lower dynamic zones, were separated on the basis of differences in the duration of annual inundation. Correlations between flow variables weakened higher up the bank and there was also no compelling evidence to suggest that floods with a return period of 1:10 to 1:20 years control the structure of the riparian zones (Boucher 2002; King *et al.* 2008). This suggests that factors other than river flow come into play higher up the bank, which again concur with the ideas of Silvertown *et al.* (1999) and Francis (2006), who showed that plant induced factors are more important for determining riparian structure there. If anything, these large floods reset the entire riparian area by uprooting large trees and mobilising large volumes of alluvial sediments (Dollar and Rowntree 2003). Thus, although it is unlikely that floods of this magnitude contribute toward the separation of the zones, they are responsible for eliminating terrestrial species that become established in the riparian area (Parsons *et al.* 2005) and have been shown to also limit recruitment of invasives (Foxcroft *et al.* 2008), a topic that was investigated further in Chapter 6. Terrestrialisation, the recruitment of incidental species into the riparian area, following an absence of large floods can have considerable knock-on effects, such as changes to the grazing patterns of large herbivores, which can lead to over grazing of palatable species that changes litter quality and may increase the incidence of fire (Naiman et al. 2008).

From an environmental flow perspective, the results indicate that duration of inundation is an important consideration in flow assessments and monitoring. Seasonal wetting maintains soil moisture levels for obligate riparian species and is considered to be particularly important for recruitment (Boucher 2002, Brown and King 2006). The boundary between the lower dynamic and the lower zone is maintained by the 1:2 year flood (Boucher 2002), which is also responsible for maintaining channel form (Gordon *et al.* 1992; Dollar and Rowntree 2003). If the annual periods of inundation are decreased through water abstraction the width of the zone of obligate species will shrink leaving an area that is not entirely suitable for facultative or incidental species, provided larger floods are still maintained. The result could be a weakened wet bank community within 1.5 m of the wetted channel edge that could results in bank instability, since riparian pioneers are known to be good bank stabilisers (Karrenberg *et al.* 2002; Kotschy and Rogers 2008; Sieben and Reinecke 2008). This area

would however provide fertile ground for alien species (Chapter 6) and might results in a lower yield for harvested marginal zone species by subsistence users (Mbaiwa 2004).

The significant correlations between location of the wet bank lateral zones and the flow regime are highly relevant in regions such as southern Africa, where there is typically a dearth of daily hydrological data. For instance, discharge was gauged at *ca.* 880 stations at 1975 (Wessels and Rooseboom 2009) but currently data are readily available for 254 online and of these, fewer have continuous observed records longer than 30 years. This means that flow data, used for environmental flow assessments and related ecological studies in these countries, often first has to be simulated at a monthly levels using rain-fall runoff data (Pitman 1973) and then disaggregated into daily data using a 'nearby' flow station, which may be in the neighbouring basin (e.g., Brown *et al*. 2006). In addition, most of these are located on mainstem rivers, with relatively few on the tributaries that feed them and that may have markedly different hydrological regimes. This lack of data severely hampers the ability of the authorities to set realistic environmental flow targets for maintaining the ecological condition of the nation's rivers. The demonstrated links between the lateral zones of riparian vegetation and the timing and magnitude of river flow passing a site can be used to either simulate or validate wet and dry season low flow discharge (using the marginal zone); the magnitude and duration of the intra-annual floods (using the division between the marginal zone and the lower dynamic zone), and the size of the 1:2 year flood, using the division between wet and dry bank. Indeed, there are examples where hydrological data provided for an environmental flow site have been sent back for review, and subsequent correction, based on a mismatch between hydraulic computations and vegetation and geomorphological signals at the site (Prof. C. Brown, UWC, pers. comm.). The position of lateral vegetation zones does not allow the zones to be used to determine the seasonal timing (i.e., the month of year in which they typically occur) of these flows, although its stands to reason that the timing of the floods may be linked to plant phenology, particular seed set and distribution (Chapter 5). With further supporting data, it may also be possible to use zonal patterns in riparian community structure, and the associated average conditions about inundation duration and flood recurrence, to estimate hydraulic conditions at rivers without having to undertake hydraulic modelling, which would greatly reduce the cost, and thus the coverage, of such assessments, be they for setting environmental flows or monitoring their efficacy.

5 Functional differences between lateral zones in Fynbos Riparian Vegetation

Karen Esler, Cate Brown and Jackie King are co-authors as each contributed towards the concepts therein and reviewed the manuscript. Martin Kidd assisted with statistical analyses. Klaudia Schachtschneider processed and provided ecophysiological data.

With regard to the sections listed below, the nature and scope of my contribution were as follows:

Section	Page number	Nature of contribution	Extent of contribution
5.3.4	68	Data collection	10%
5.3.4	68	Data analysis	70%
5.4.3	72-75	Results of analysis	30%

The following co-authors have contributed to the sections listed below:

Co-author	Email	Section	Nature of contribution	Extent of contribution
K Schachtschneider	KSchact@csir.co.za	5.3.4	Data preparation	90%
M Kidd	Mkidd@sun.ac.za	5.3.4	Data analysis	30%
M Kidd		5.4.3	Results of analysis	70%

Signature of candidate:

Date: 23 October 2013

The undersigned hereby confirm that:

1. The declaration above accurately reflects the nature and extent of the contributions of the candidate and the co-authors in the listed sections,
2. No other authors contributed to the listed sections besides those specified above, and
3. Potential conflicts of interest have been revealed to all interested parties and that the necessary arrangements have been made to use the material in the listed sections of the dissertation.

	Signature	Institutional affiliation	Date
Martin Kidd		University of Stellenbosch	
Klaudia Schachtschneider		CSIR	

5.1 Introduction

Plants persist by exploiting favourable conditions and resisting unfavourable conditions (Resh *et al.* 1998). In riparian zones along headwater streams, where the resource- and disturbance-gradients are marked, the relative requirements and tolerances of plant species results in distinct zonation of the community (Chapters 3 and 4), with the locations of the wet-bank zones controlled by the plants' adaptions to the river's flow regime (Chapter 4) and those of the dry bank zones presumably more dependent on different persistence mechanisms and/or competition for resources (Silvertown *et al.* 1999; Francis 2006).

When plants compete for resources, such as nutrients and water, niches are tightly defined with little overlap but when resources are plentiful and competition low, species' distributions extend beyond their specific niches (Silvertown *et al.* 1999). Thus, Silvertown *et al.* (1999) propose that competition between plants influences community structure to a greater extent higher up the bank because hydrological disturbances occur less frequently; lower down the

bank hydrogeomorphological disturbances override biological factors that influence plant growth and persistence.

Data on phenology and autecology, such as seed germination, viability and dispersal studies, are often used to document plant community responses to changing environmental conditions (Leith 1974; Pierce 1984). Some of this work, done for the links between riparian vegetation, flow and phenology (Reich and Borcherd 1984; Swift *et al.* 2008; Misson *et al.* 2009; Crous 2010; and Palta *et al.* 2012), addresses the temporal occurrence of life history phases in relation to hydrological pattern, referred to as phenophases. The onset of phenophases has been linked to *inter alia* soil moisture and cumulative warming hours (and photoperiod) for leaf growth and stem elongation (Kumerow 1983), low soil moisture in combination with short days for leaf fall (Nilsen and Muller 1980, cited by Pierce 1984) and the duration of light for flowering (Erickson *et al.* 1980, cited by Pierce 1984). Other factors affecting phenology are biological, and include pollinators, dispersers, predators and competition for resources (Pierce 1984). Phenophase development may also be staggered through a population in response to temporal gradients in resources. For instance, the rate of shoot growth may vary within the same species at different altitudes and/or in different climatic zones (Fritts 1976). Given the steep lateral gradients in resources on river banks, localised temporal staggering in phenophases may be expected in riparian communities, particularly following flooding as physical conditions (soil moisture, oxygen availability, depth to groundwater, decomposition rates and nutrient availability) experienced by individual plants may change rapidly, resulting in a favourable windows for growth or reproduction (Merrit and Wohl 2002).

The outcome of ground-breaking studies linking plant phenophases to the flow regime of rivers in cottonwood floodplain forests of North America was discussed in Chapter 2. There, cohorts of seedlings establish after floods at positions low enough to provide adequate moisture and high enough to avoid scour (Amlin and Rood 2002). Through time, cohorts develop in positions that are directly linked to historical flood events (Stromberg 1993; Stromberg and Patten 1990; Stromberg *et al.* 2007). Flooding in these rivers is regular and predictable (Rood *et al.* 1999). As a result, the recruitment 'window' of cottonwoods is narrow, and recruitment failure high if flooding is aseasonal (Naiman *et al.* 2005). The Recruitment-box Model (Chapter 2) derived from these studies is well-established, and as such provided a useful point of reference for the assessment of functional differences between lateral zones in Fynbos Riparian Vegetation. This is particularly the case because of the large differences between the flood plain forests on which the Recruitment-box Model was developed and the rivers in this study (see Section 2.1.1).

The rivers in this study differ considerably from those where the Recruitment-box Model was developed, such as the Colorado River where cottonwoods occur. They are steep, have constrained stable channels comprised of large-calibre sediments that do not migrate laterally (Dollar and Rowntree 2003) and lack floodplains (Davies *et al.* 1995). Although seasonal rainfall patterns in the south-western Cape are reliable (Cowling *et al.* 2004), the timing of large floods is unpredictable and year-on-year flood volume is erratic (Gordon *et al.* 1992; Ractliffe 2009). The pressure gradients between plants and the surrounding air are also greater, than in moist temperate regions (Smith *et al.* 1998). The prevailing conditions of these systems make them Mediterranean Type Ecosystems (MTE), such as those in California, Spain and Chile (Cowling *et al.* 2004), which are characterized by hot dry summers and wet cold winters (Gasith and Resh 1999).

If the Recruitment-box Model applies to Western Cape rivers, then the phenology of the riparian plants should coincide with flows that favour dispersal to preferred locations, plants that disperse seed at different times of the year should be located at different stages on the banks (elevation above water level; Merrit and Wohl 2002) and the temporal order of seed set should start with dry bank species at the onset of flooding and end with wet bank species after flood recession. In addition, annual cohorts of recruits should be clearly identifiable at

specific bank position. Evolutionary theory states that floods may drive adaptations for synchronised reproductive traits if they occur frequently, are large in magnitude and predictable (Lytle and Poff 2006). The variability in the flow regimes, in particular compared with that in the cottonwood floodplain forests of North America, suggests that specialist recruitment traits, in terms of synchronised life histories to flow, may not be advantageous for plants along Western Cape rivers since generalist traits are expected in species that inhabit heterogeneous environments (Devictor *et al.* 2008). Alternately, it may that a combination of sexual and asexual reproductive strategies, such as re-sprouting (Holmes and Richardson 1999), clonal growth (Duhovnikoff *et al.* 2005) and the dispersal of vegetative diaspores (Nilsson 2002) is more successful.

To test which of these situations apply, the timing of phenophases, relative to their position on the river banks, was investigated for three, commonly-occurring Fynbos riparian trees (Mucina and Rutherford 2006): the Cape willow, *Salix mucronata* Thunb.; the lance-leaf myrtle, *Metrosideros angustifolia* (L.) Sm; and the wild almond, *Brabejum stellatifolium* L.. *Salix mucronata* Thunb is a wet-bank plant with pioneering traits (Karrenberg *et al.* 2002) that include rapid growth and the ability to reproduce both sexually, via hydrochorous seed dispersal, and also asexually, via the dispersal of vegetative plant fragments that root when buried. This small tree grows to 12 m (Goldblatt and Manning 2000) and occurs in the wet bank (Chapter 3) and on mid-channel islands throughout South Africa. Seeds are covered in woolly hairs (van Wyk and van Wyk 1997) and are dispersed by wind (Thomas *et al.* 2007) and water (Karrenberg *et al.* 2002). The lance-leaf myrtle, *Metrosideros angustifolia* (L.) Sm., and the wild almond, *Brabejum stellatifolium* L., are dry bank species (Chapter 3). *Metrosideros angustifolia* L. (Sm.) is a small tree that grows to 7 m (Goldblatt and Manning 2000) and is restricted to sandstone slopes of Western Cape rivers. Seeds are small (4 mm), brown and hard (van Wyk and van Wyk 1997) and are reportedly wind dispersed (Givnish and Renner 2004) but lack the characteristic fluffy appearance of wind dispersed species, and so may be dispersed by water or animals. *Brabejum stellatifolium* L. is a spreading multi-stemmed tree that grows to around 8 m (Goldblatt and Manning 2000) and is restricted to Western Cape rivers. The fruits are almond shaped, single seeded, covered in velvety hairs (Van Wyk and Van Wyk 1997) and are water dispersed (Palgrave and Palgrave 2002).

In this chapter the key questions (Figure 1.1) were, “Does river flow influence growth of riparian species?” and “Do occupants of different zones exhibit functional differences?” These key questions were incorporated into the design and testing of three hypotheses:

- If the flow regime controls plant dispersal into lateral zones then:
- each of the three species should be dispersed preferentially into the zone in which it occurs most frequently; and
- the periods of flowering and seed set should be longer than those of cottonwoods to accommodate the unpredictability of winter flooding, and the order of seed set should be 1) dry bank prior to flood onset, and 2) wet bank, following flood recession.
- If the flood disturbance controls plant survival in lateral zones then plants in the wet bank should invest growth towards length rather than girth to bolster flexibility, whereas those in the dry bank should invest in girth to be able to withstand the force of occasional floods. In addition, wood density should be lower for the more flexible wet bank plants when compared to the more rigid dry bank plants.
- If water availability controls plant survival in lateral zones, tolerance to drying out should be lower for wet bank plants and higher for dry bank plants. Thus, reduced summer base flows should retard growth of the wet bank species more than that of the dry bank species.

5.2 Study sites and species

Phenological and physiological data were collected at four sites on the Molenaars and Sanddrifskloof Rivers. Paired sites were situated upstream and downstream of an abstraction weir. The four sites were situated on two perennial tributaries of the Breede

River in the south-western Cape of South Africa (Table 5.1) in wilderness areas and in close proximity to flow gauges (Figure 5.1) with reliable hydrological records in excess of 30 years. The Molenaars River site (M-up) was situated downstream of Mol1 where hydraulics were modelled for Chapter 4 and in close proximity to the same gauge that provided hydrological data.

Table 5.1 Study site locations.

River	Site	Position	Latitude	Longitude
Molenaars	Gauge H1H018	Upstream of M-up and M-do	-33.724008	19.169724
	M-up	Upstream of abstraction	-33.719877	19.18819
	M-do	Downstream of abstraction	-33.703436	19.232554
Sanddrifskloof	Gauge H2H004	Upstream of S-up and S-do	-33.485484	19.529077
	S-up	Upstream of abstraction	-33.486433	19.529328
	S-do	Downstream of abstraction	-33.487186	19.529822

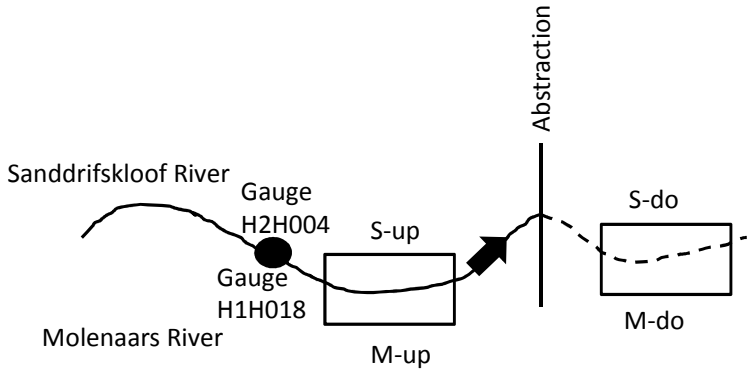

Figure 5.1 Site orientation in relation to the Molenaars and Sanddrifskloof River gauges. Arrow indicates downstream flow. Site codes as per Table 5.1.

5.3 Methods

5.3.1 Hydrology

Hydrological data for the Molenaars River were provided by Chapter 4 and the same data reduction techniques were used to synthesize the hydrological record of the Sanddrifskloof River obtained from the Department of Water Affairs (DWA, http://www.dwaf.gov.za/Hydrology/). The Indicators of Hydrologic Alteration (IHA) software package (The Nature Conservancy 2009) was used to generate indicators of flow variability[16] for the three rivers. The following statistics of flow variability and predictability were generated (after Poff and Ward 1989):

- Mean daily flow.
- Predictability of flow, defined by Colwell's index (1974). Values range between 0 - 1, values closer to 1 being more predictable. This index consists of two components: constancy, reflecting changes through time, and contingency, reflecting whether these changes occur regularly or stochastically.
- Coefficient of Variation (CV) of mean daily flow, measures variation about the mean and so is insensitive to temporal patterns. Higher values are more variable.

[16] The IHA software does not generate a value for the interval between floods. We calculated this from two other indicators generated by IHA by subtracting the timing of the 1:2 year flood from that of the extreme low flow period. This value reflects the time in days between flood recession and flood onset.

- Mean flood duration, the average number of days that flows are greater than the 2-year flood.
- Flood predictability, the maximum proportion of floods that occur over any 60 day period. The index ranges from 0.167 (random) to 1 (perfectly predictable).
- Zero flood days, the average number of days that no floods were recorded.
- Flood interval, the median interval between flood periods.
- Flood time, the median Julian day on which floods have occurred.

The results were compared with an unregulated section of the Colorado River, where cottonwoods occur (Poff and Ward 1999). Mean monthly discharge was calculated from the daily time series and plotted for the upstream sites on the Molenaars and Sanddrifskloof Rivers. Monthly spot measurements of discharge were recorded at both downstream sites on the Molenaars and Sanddrifskloof Rivers.

5.3.2 Plant distribution and lateral zone hydraulics

Data on the distribution of the three tree species along south-western Cape rivers (Table 3.1) were obtained from Chapter 3 while average flood recurrence intervals and inundation durations for the wet and dry bank were obtained from Chapter 4. The plant distribution data was separated into three life stages; trees > 2.0 m in height, saplings 2 > height > 0.3 m and seedlings < 0.3 m in height.

5.3.3 Plant phenology

Phenology measurements were collected from ten trees of *Salix mucronata, Metrosideros angustifolia* and *Brabejum stellatifolium*, at both upstream and downstream sites on the Molenaars and Sanddrifskloof Rivers (M-up, M-do, S-up and S-do). Monthly measurements of stem-tip growth (length) were made from marked positions of five branches on each tree, one from each different cardinal direction (Disalvo and Hart 2002) and an additional branch. Repeat measurements were made monthly on the same branch. Since the plants are multi-stemmed, trunk girth was not a practical measurement so girth measurements were made at the base of each measured branch (Hughes *et al.* 2000). The proportions of flowers, fruits and seeds on *S. mucronata, M. angustifolia* and *B. stellatifolium* per canopy were estimated. Since no seed dispersal data were collected, the assumption was made that the presence of ripe seed on a tree indicated the readiness to disperse. Ten sets of pheno-data were collected, after floods had receded in Spring (September 2011) up to flood onset the following Winter (June 2012)[17].

The abundance of flowers, fruits and seeds were reduced to average values for each species per site per month and tabulated. Changes between phenophases over the hydrological year were plotted on a Molenaars River hydrograph to illustrate potential links between the onset of flowering and seeding with high and low flow periods.

5.3.4 Plant physiology

Three physiological indicators of tolerance to drying out were chosen on the basis of their simplicity, cost effectiveness and value gained in terms of once off measurements: specific leaf area (SLA), level of stable $\delta^{13}C$ isotopes and wood density (Schachtschneider 2009). SLA is the ratio of wet leaf area to dry leaf mass (Amanullah *et al.* 2007). It is an indicator of growth vigour and can be related to water availability with the support of other evidence. Reduced water availability is said to increase leaf thickness and reduce size, resulting in a

[17] Thirteen set of phenol-data were actually collected, during July, August and October 2012 but these data sets were incomplete as two of the study sites were inaccessible during high flow. It was not possible to include these data into the analyses.

lower SLA (Rood *et al.* 2003). Carbon isotopes are an index of water use efficiency and time integrated carbon assimilation (Pockman and Sperry 2000). Plants restrict gas exchange by closing their stomata when less water is available and this results in less negative $\delta^{13}C$ values. Wood density is an indicator of xylem traits that relate to water stress tolerance, such as P_{min}, vessel area and percentage fibre wall (Jacobsen *et al.* 2007). Plants that experience drying out regularly are said to have thicker xylem vessels to reduce the chance of total embolism occurring (Hacke *et al.* 2000). Ten plants of each of the three species were selected at the up and downstream sites on the Molenaars and Sanddrifskloof Rivers (M-up, M-do, S-up and S-do). Thereafter:

- For the measurement of SLA, 35 mature and fully-exposed leaves were randomly selected and collected per tree. The leaves were sealed in plastic, cooled and transported back to the laboratory where, within 48 hours, the leaflets were separated from the rachis and pinnae, spread out next to a ruler on a white background and photographed. Average leaf area per specimen was determined by analysing the photographs using Sigma Scan Pro 5. The leaves were then oven dried at 70°C for 48 hours, after which they were weighed to determine dry mass. SLA was expressed as leaf area/dry weight ($cm^2.g^{-1}$).
- For stable carbon isotope analysis, 20 fully expanded, mature leaves were collected from each tree. Prior to mass spectrometry, the leaves were oven dried at 70°C for 24 hours and ground to a fine powder using a Retsch MM200 ball mill (Retsch, Haan, Germany). Samples were analysed by an independent laboratory at CSIR, Pretoria, South Africa.
- For wood density, one twig was cut from each tree (10 cm x 0.7 cm diameter) and transported back to the laboratory frozen. The twigs were saturated in degassed water for 24 hours, in order to obtain maximum weight (Jacobsen *et al.* 2007). They were then cut to a length of 2.4 cm and the pith and bark were removed with a razor blade. Wood volume was determined by displacement in a graduated cylinder (Jacobsen *et al.* 2007). The wood was then oven dried for 24 hours at 75°C and the dry mass weighed. Wood density was expressed in $g.cm^{-3}$.

General discriminant models (see Section 3.2.2.2) were used to test the variance about the means of growth and physiological measures between species, sites and rivers. Univariate tests of significance provided evidence for differences between rivers, river position (upstream versus downstream), species and the day of measurement (season).

5.4 Results

5.4.1 River hydrological characteristics

M-up and S-up experienced similar hydrological conditions in the winter with floods in June to September that receded through spring (October and November; Figure 5.2). The flow at M-up was unregulated, and summer low flows occurred from January to March. Summer base flow was elevated at S-up as irrigation releases are made from a reservoir upstream. This study focussed on the effect of abstraction downstream so elevated base flow upstream at S-up was not problematic. M-do received about one third of its natural summer flows, while the river was dry at S-do during spring and summer (Table 5.2).

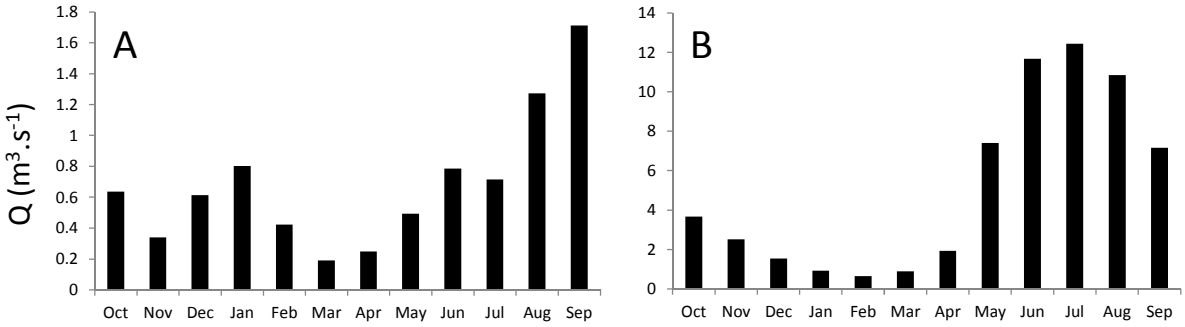

Figure 5.2 **Annual hydrographs for upstream sites on A) the Molenaars and B) Sanddrifskloof rivers. Data are monthly average discharge (Q) in m3.s^{-1}.**

Table 5.2 **Instantaneous discharge (Q = m3.s^{-1}) at sites upstream and downstream of abstraction points on the Molenaars (M-up, M-do) and Sanddrifskloof (S-up and S-do) rivers. - indicates river flow was too strong to record manually. Site codes as per Table 5.1.**

River	Site	2011				2012					
		Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Molenaars	M-up	16.4	3.67	2.53	1.54	0.93	0.65	0.35	4.80	2.79	7.05
	M-do	-	1.36	0.92	0.57	0.31	0.24	0.14	-	1.03	-
Sanddrifskloof	S-up	0.93	0.64	0.35	0.61	0.80	0.42	0.42	0.72	0.65	1.66
	S-do	0	0	0.25	0	0	0	0	0	0	0.14

Indicators of river flow variability and predictability for the Molenaars, and Sanddrifskloof Rivers were compared to the Colorado River in North America (Table 5.3). The coefficient of variation about mean daily flow and the number of days that experience flooding (flood duration) were higher for the South African rivers while flood predictability, the average number of days a year where no flooding was experienced (zero flood days) and the average number of days between periods of flooding (flood interval) were lower.

5.4.2 Flowering and seed set at the Molenaars and Sanddrifskloof Rivers

S. mucronata flowered in early spring (September-October) on both rivers (Figure 5.3 and Appendix Table 8.5) as flows receded after winter floods. More branches flowered in greater abundance at the Molenaars than at the Sanddrifskloof River. Fruits (green seed) were only present at the Molenaars River in late spring (October-November). Seed ripened over two months in early summer (December-January) and were dropped during January, coinciding with summer low flow. More *M. angustifolia* branches flowered in greater abundance at the Molenaars than at the Sanddrifskloof River during summer (December-March). Fruits were present during autumn (April-May) at the approach of the wet season (Figure 5.3 and Appendix Table 8.6). Seeds were present and released over a four month period during winter high flow (June-September). *B. stellatifolium* trees flowered from spring to early summer (September-January). Fruits (green) were sparse and only recorded at the Sanddrifskloof River during summer (January-March). Seed (ripe fruits) were present and released during autumn (April-May) at the approach of the wet season (Figure 5.3 and Appendix Table 8.7).

Table 5.3 Comparison of hydrological characteristics of the study rivers in South Africa and the Colorado River in North America (Poff and Ward 1998).

	North America	South Africa	
	Colorado River	Molenaars River	Sanddrifskloof River
Gauge station	09010500	H1H018	H2H004
Years in record	30	42	35
Area (km^2)	138	111	177
Mean daily flow ($m^3.s^{-1}$)	1.8	5.0	1.0
Predictability of flow	0.66	0.47	0.42
CV daily mean flow	0.38	2.53	1.88
Flood duration (days)	10.9	17.0	29.5
Flood predictability	1.0	0.33	0.32
Zero flood (days)	331	22	10
Flood interval (days)	339	118	81
Flood time (Julian day)	254	186	194

5.4.3 Growth in length and girth at the Molenaars and Sanddrifskloof Rivers

There were no discernible differences in cumulative branch growth in terms of length or girth between the upstream and downstream sites at either river (Table 5.4). More than half of all branches that grew in length also increased in girth. This was true for all three species. In general more *B. stellatifolium* and *M. angustifolia* branches grew in girth than in length, while more *S. mucronata* branches grew in length than in girth. Some *S. mucronata* branches, and one *M. angustifolia* branch, were shortened due to stem breakage and a small fraction of these also reduced in girth. A fixed effect test for the effect of four factors (river, position, species and sample day) on cumulative growth in length was highly significant ($p < 0.001$); changes in length were not discernible between upstream and downstream sites at either river (Figure 5.4). A fixed effect test for the effect of river, position, species and sample day on cumulative growth in girth was not ($p < 0.069$); changes in girth were not discernible between upstream and downstream sites on either river (Figure 5.5).

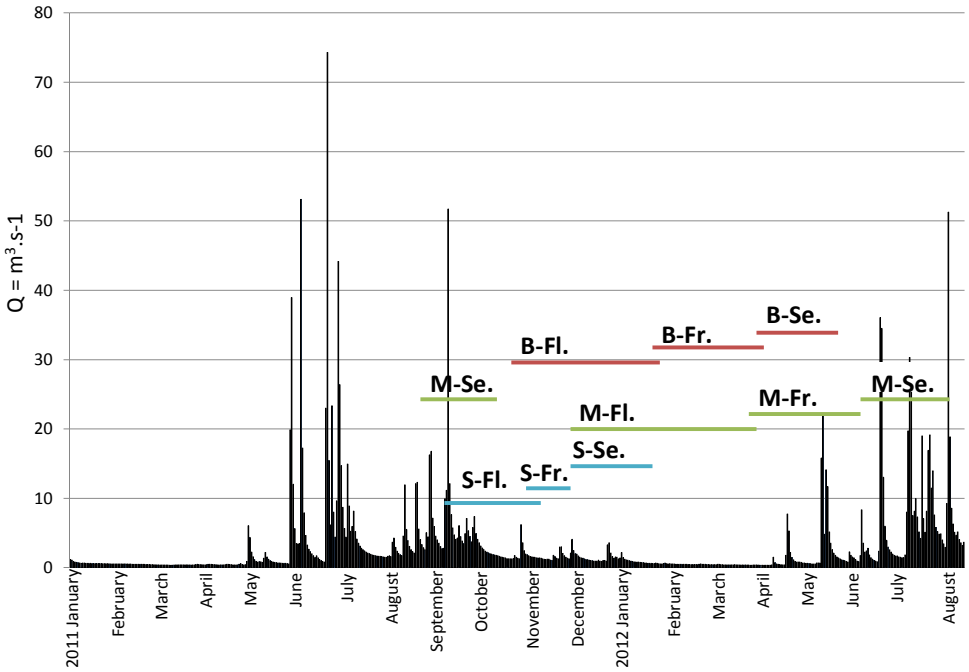

Figure 5.3 **Hydrograph of daily average discharge (Q) at M-up with timing of flowering (Fl.), fruit (Fr.) and seed (Se.) set for *Salix mucronata* (S, blue), *Metrosideros angustifolia* (M, green) and *Brabejum stellatifolium* (B, red). *Brabejum* seed data are from S-up since none were recorded at M-up.**

Table 5.4 **The number of branches where length or girth changes were recorded at M-up, M-do, S-up and S-do. (+) = increase, (-) = decrease, (×) = no change. n = total branches measured. Site codes as per Table 5.1.**

Site	Tree	Length (n=15)			Girth (n=15)			Both (n=15)		
		+	-	×	+	-	×	+	-	×
M-up	*B. stellatifolium*	3		12	7		8	2		7
	M. angustifolia	9	1	5	12	1	2	9		2
	S. mucronata	12	2	1	9	3	3	9	2	1
M-do	*B. stellatifolium*	3		12	9	3	3	2		8
	M. angustifolia	5		10	7		8	3		6
	S. mucronata	14		1	12		3	11		
S-up	*B. stellatifolium*	10		5	14		1	9		
	M. angustifolia	9		6	10	1	4	6		
	S. mucronata	9	3	3	7	2	6	6	1	1
S-do	*B. stellatifolium*	7		8	7		8	4		5
	M. angustifolia	10		5	13		2	8		
	S. mucronata	9	1	5	11	2	2	9		2

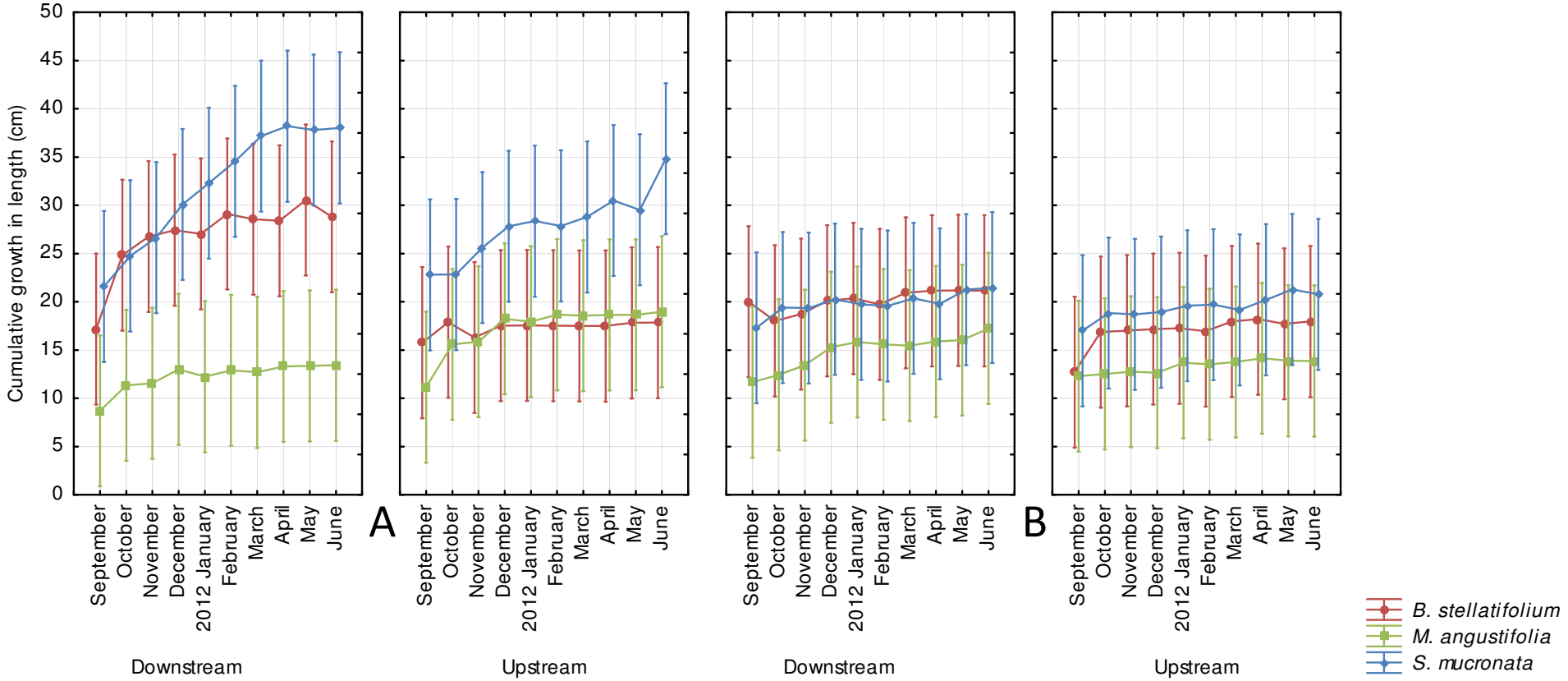

Figure 5.4 **Changes in length of *B. stellatifolium*, *M. angustifolia* and *S. mucronata* branches at both sites on the Molenaars (A) and Sanddrifskloof (B) Rivers respectively. Vertical bars are 95% confidence limits.**

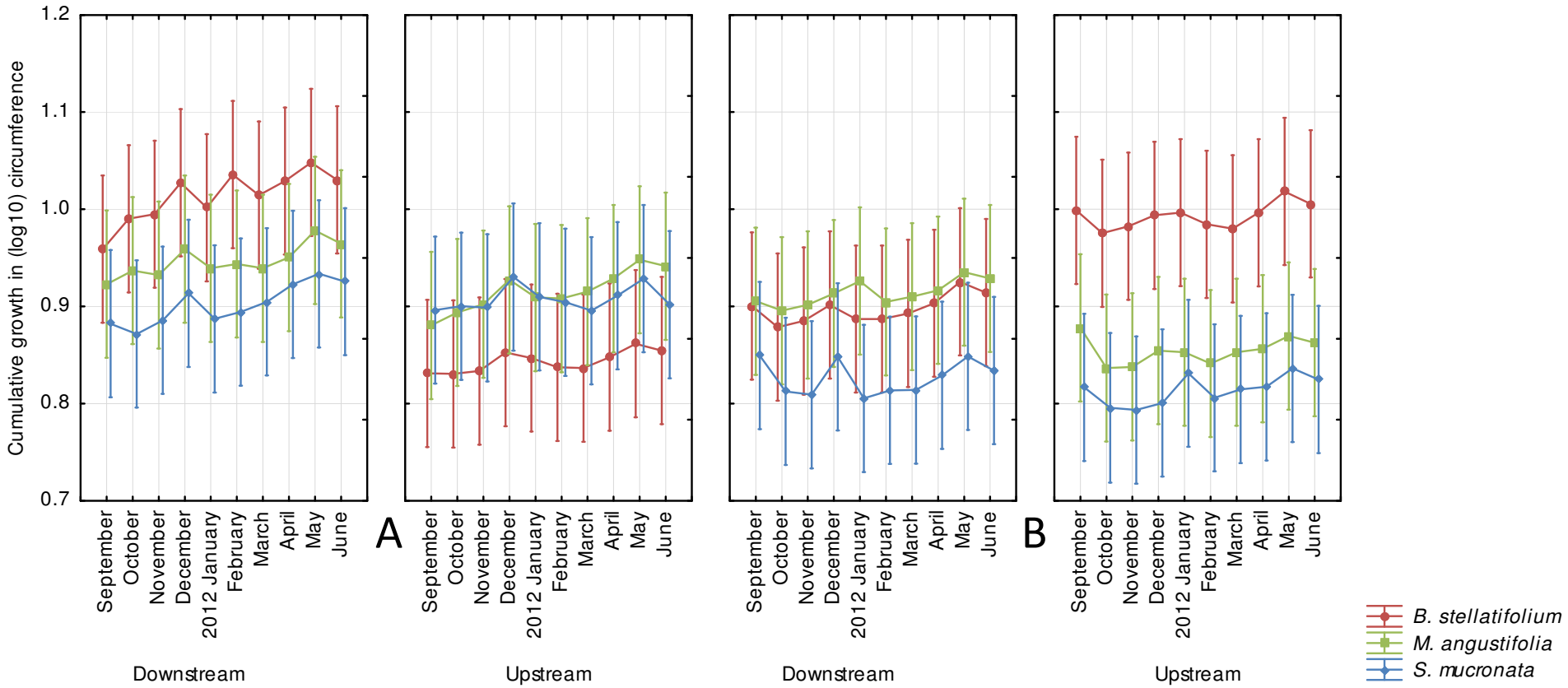

Figure 5.5 **Changes in girth of *B. stellatifolium*, *M. angustifolia* and *S. mucronata* branches at both sites on the Molenaars (A) and Sanddrifskloof (B) Rivers respectively. Vertical bars are 95% confidence limits.**

5.4.4 Tolerance to drying out

Specific Leaf Area (SLA, $cm^2.g^{-1}$) was significantly different between species ($p < 0.001$) being highest for *S. mucronata*, intermediate for *M. angustifolia* and lowest for *B. stellatifolium* (Figure 5.6). There were no discernible differences between upstream and downstream sites on either river.

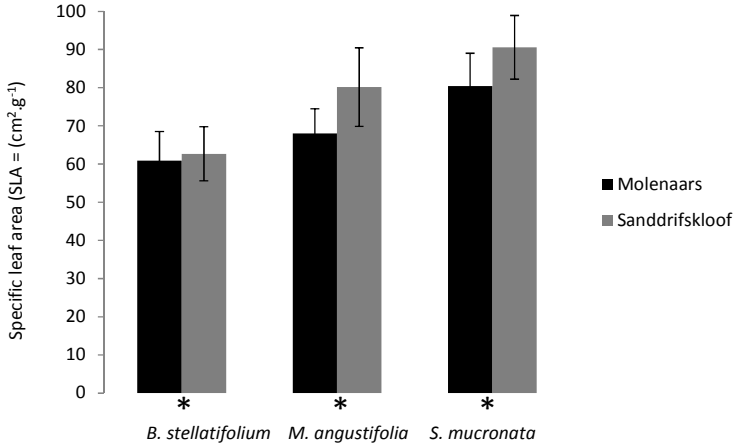

Figure 5.6 **Specific Leaf Area ($cm^2.g^{-1}$) of *B. stellatifolium*, *M. angustifolia* and *S. mucronata* leaves at the Molenaars and Sanddrifskloof Rivers. Vertical bars are 95% confidence limits. * = significant differences between species.**

A fixed effect test for the effect of river, position, species and sample day on wood density ($g.cm^{-3}$) was significant at the 10% level ($p < 0.069$). *S. mucronata* wood was less dense than *B. stellatifolium* and *M. angustifolia* at both sites on the Molenaars River (Figure 5.7) while *M. angustifolia* wood was most dense downstream on the Sanddrifskloof River (Figure 5.8).

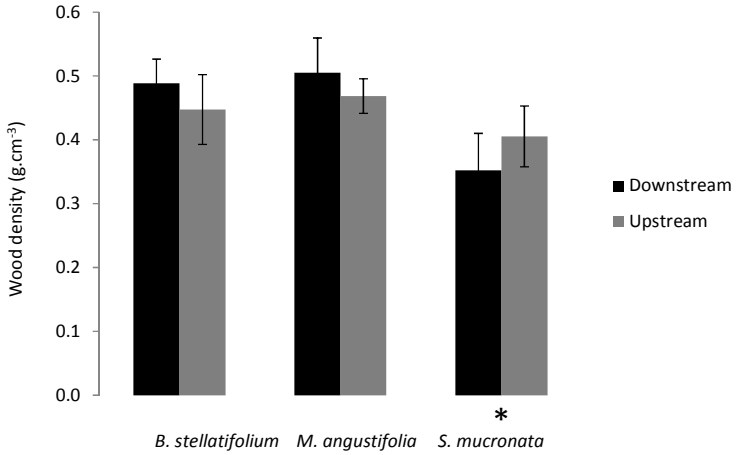

Figure 5.7 **Wood density ($g.cm^{-3}$) of *B. stellatifolium*, *M. angustifolia* and *S. mucronata* branches at the Molenaars River. Vertical bars are 95% confidence limits. * = significant differences between *S. mucronata* and the other species.**

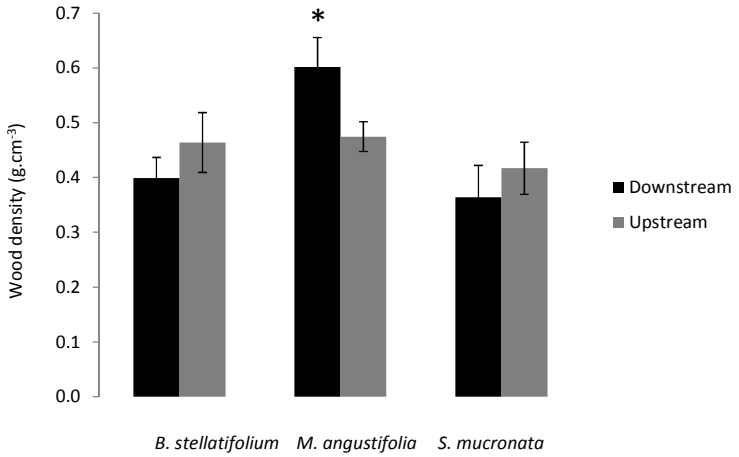

Figure 5.8 **Wood density (g.cm^{-3}) of *B. stellatifolium*, *M. angustifolia* and *S. mucronata* branches at the Sanddrifskloof River. Vertical bars are 95% confidence limits. * = significant differences between downstream *M. angustifolia* and the other species.**

The level of carbon isotopes ($\delta^{13}C$) differed between species ($p < 0.001$, Figure 5.9). These levels were least negative for *M. angustifolia*, intermediate for *B. stellatifolium* and most negative for *S. mucronata*. There were also differences between *B. stellatifolium* and *S. mucronata* between the rivers ($p < 0.001$), but not for *M. angustifolia*. There were no discernible differences between river position.

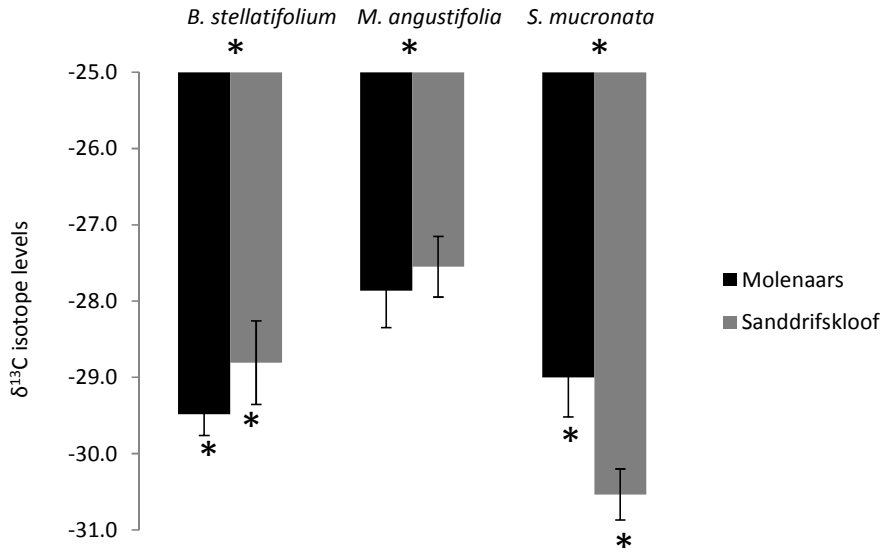

Figure 5.9 **$\delta^{13}C$ isotope levels present in *B. stellatifolium*, *M. angustifolia* and *S. mucronata* branches at the Molenaars and Sanddrifskloof Rivers. Vertical bars are 95% confidence limits. * = significant differences between species and also between rivers for *B. stellatifolium* and *S. mucronata*.**

The three measures of tolerance to drying were compared. In all three cases *S. mucronata* scored the lowest in having the highest SLA, the lowest wood density and the most negative values for $\delta^{13}C$ (Table 5.5). SLA and wood density indicated that *M. angustifolia* was less tolerant than *B. stellatifolium* while the level of $\delta^{13}C$ suggests that *M. angustifolia* was more tolerant.

Table 5.5 **Relative scores about tolerance to drying out for *S. mucronata*, *M. angustifolia* and *B. stellatifolium*.**

Indicator of drying tolerance	Relative score
Specific leaf area	*S. mucronata* < *M. angustifolia* < *B. stellatifolium*
Wood density	*S. mucronata* < *M. angustifolia* = *B. stellatifolium*
$\delta^{13}C$ isotope levels	*S. mucronata* < *B. stellatifolium* < *M. angustifolia*

5.4.5 Recruitment of the three species into the wet and dry banks

Seedlings and saplings of *S. mucronata* were more abundant in the wet bank (Figure 5.10). Most seedlings and saplings of *B. stellatifolium* and *M. angustifolia* were found in the transitional area between the wet and dry banks and were equally abundant in both the wet and dry banks.

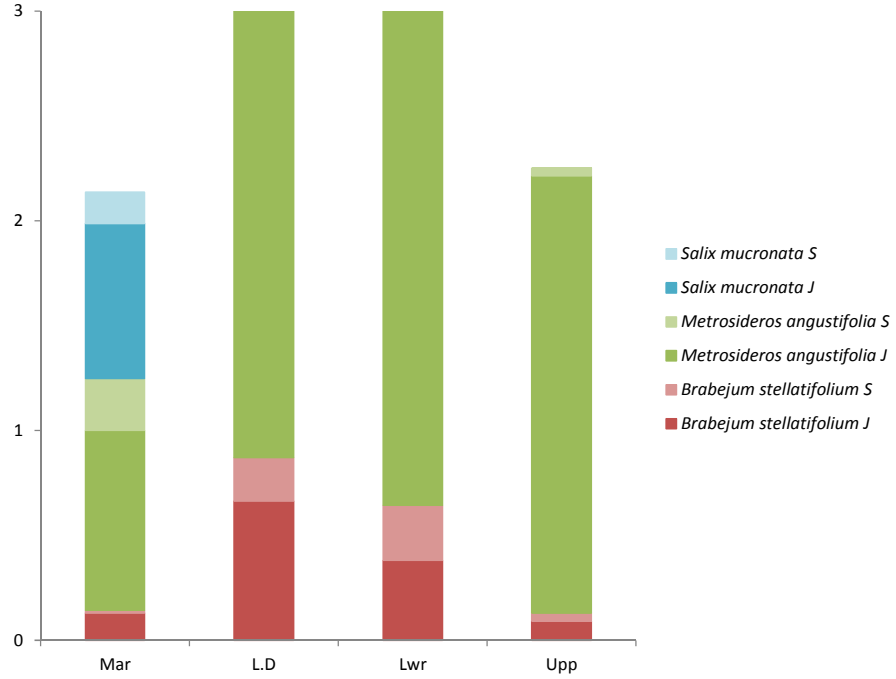

Figure 5.10 **Average cover (%) abundance of *B. stellatifolium, M. angustifolia* and *S. mucronata* saplings (J) and seedlings (S) into the wet and dry bank of Western Cape Rivers (data from Chapter 3). Mar (marginal) + L.D. (lower dynamic) = wet bank; Lwr (lower) + Upp (upper) = dry bank.**

5.5 Discussion

Functional differences were apparent between the three tree species that occupy different lateral zones in terms of the season of seed dispersal, growth in branch length versus girth and three measures of tolerance to drying out.

Hypothesis 1 predicted that if the flow regime controls plant dispersal into lateral zones then the three species should be dispersed preferentially into the zone in which they occur most frequently; the order of seed set should be 1) dry bank prior to flood onset, and 2) wet bank, following flood recession and the periods of flowering and seed set should be longer than those of cottonwoods to accommodate the unpredictability of winter flooding.

Salix mucronata was situated in the wet bank that was inundated but not overtopped, by intra-annual floods (Chapter 4) and like cottonwoods, is a riparian pioneer (Karrenberg *et al.* 2002). *S. mucronata* and *Populus* spp. are also in the same family and therefore similarities in their life histories may result from phylogenetic constraints rather than due to lateral zone position. As expected, *S. mucronata* seed dispersal coincided with dry-season flows and was dispersed for a similar length of time as cottonwoods: two to three months (Mahoney and Rood 1998). *S. mucronata* seedlings rely on moist conditions to establish (Guilloy *et al.* 2011) and so targeting low flows, and thus the marginal zone adjacent to the wetted edge, minimises seedling mortality by reducing the risk that seeds are deposited into the dry bank where moisture levels are too low for most of the year to support germination. Targeting the marginal zone in this way certainly minimises seedling mortality during summer but in winter these low lying seedlings will be subject to scour. This topic was not taken further in this dissertation but is the topic of another study (Magoba 2013).

M. angustifolia was situated in the dry bank (Chapter 3). Its seeds are supposedly dispersed by wind (Givnish and Renner 2004) but personal observations of clumps of seedlings at the water's edge, on the lee surface of boulders in the dry-season wetted channel and among the roots of wet bank trees, suggests otherwise. Similar observations were made by Galatowitsch and Richardson (2005). Seedlings and saplings of *Metrosideros angustifolia* were distributed across the wet and dry banks and seeds were dispersed over 4 months through the wet season, which is contrary to the predictions, but it makes sense as both the wet and dry banks were inundated by the inter-annual floods (Chapter 4, Hupp and Osterkamp 2002, Nillson and Svedmark 2002). Thus, some overlap between the wet and dry banks is to be expected as this represents a gradient of changing conditions (Chapter 3, Boucher 2002, Kleynhans *et al.* 2007). The location of the water-transported seeds observed during the study also supports the idea that seedlings of Fynbos Riparian Vegetation may preferentially recruit on stable banks or in rock fractures (Galatowitsch and Richardson 2005) rather than on recent alluvial deposits, as described for cottonwood floodplain forests (Mahoney and Rood 1995, Rood *et al.* 1999).

B. stellatifolium was situated in the dry bank (Chapter 3) and its seeds are hydrochorous (Palgrave and Palgrave 2002). Seedlings and saplings were concentrated at the boundary between the wet and dry banks, across the lower dynamic and lower zones respectively, and seeds were released over a two to three month period prior to the flood-onset. As for *M. angustifolia,* recruitment was more commonly observed among tree roots, or other vegetative cover, rather than on recent alluvial deposits.

There was no evidence to support the prediction that the length of seed release differed between the three species, despite the variability in the flooding regime; it may be that seed viability is more critical to recruitment success. Cottonwoods seeds are only viable for two to three weeks and are released over a *ca.* two month period (Braatne *et al.* 1996). Little is known about the length of time that seeds of *S. mucronata, M. angustifolia* and *B. stellatifolium* remain viable. Vosse *et al.* (2008) report that *M. angustifolia* and *B. stellatifolium* do not rely on persistent seed banks and suggest that re-sprouting is their strategy of persistence. If it can be shown that seeds of these three species persist for longer than two to three months, it would strengthen the case that the variable flow experienced by these trees may have driven alternate life history adaptations.

Hypothesis 2, which predicted that *S. mucronata* should invest growth towards length and flexibility, and *M. angustifolia* and *B. stellatifolium* should invest in girth to be able to withstand the force of occasional floods, was upheld. More stems of *M. angustifolia* and *B. stellatifolium* grew thicker than longer, whereas stems of *S. mucronata* tended to be longer rather than thicker. Contrary to expectations, however, *S. mucronata* stems did not seem to be particularly flexible. Stem snap (breaking of branches) was recorded regularly for the *S.*

mucronata trees but only once for *M. angustifolia* and not at all for *B. stellatifolium*. Exposure of *S. mucronata* to regular flooding pruned branches back, which were readily replaced (Rood *et al.* 2000). This is part of the pioneering adaptations of *Salix* spp. (Guilloy *et al.* 2011) as these branches then root if buried at suitably wet locations (Nilsson and Svedmark 2002). Thus, *S. mucronata* displayed two recruitment strategies linked to the flow regime. It reproduced vegetatively, by releasing branch fragments during high flow, and sexually, by releasing seeds at low flow (Douhovnikoff *et al.* 2005). The shorter, stouter, denser (Crous *et al.* 2012) branches of *M. angustifolia* and *B. stellatifolium* did not display stem snap. It is not known whether these two species disperse branch fragments as vegetative propagules, but they can and do re-sprout from epicormic stem tissue if knocked over by floods (Holmes and Richardson 1999). Thus, although the predictions were not all supported, all three species showed adaptations to survive floods, the nature of which was linked to their zonal location.

As predicted in Hypothesis 3, higher wood density, smaller leaf area and less negative values for $\delta^{13}C$ isotopes (Woodborne *et al.* 2003) indicated that *M. angustifolia* and *B.* stellatifolium were more tolerant of dry conditions than *S. mucronata.* It was not possible to separate *M. angustifolia* and *B. stellatifolium* from one another in terms of tolerance to drying,, which concurs with the findings of Swift *et al.* (2008) that *B. stellatifolium* has a greater tolerance to catastrophic embolism than *M. angustifolia*, one adaptation to drying, but that *M. angustifolia* can also cope with dry conditions by thickening its xylem when water is limited. Crous *et al.* (2012) also demonstrate differences in adaptation, but equal tolerance to drying, for *B. stellatifolium* and *M. angustifolia* using measures of hydraulic conductivity and wood density.

Finally, it was expected that artificially reduced summer flows would retard growth of *S. mucronata* more than that of *M. angustifolia* and *B.* stellatifolium. However, we found no significant differences in growth rates between trees at sites with natural summer flows and those at sites where the entire summer flow had been abstracted. In retrospect, this was not surprising as riparian plants are known to access sub-surface flow (Castelli *et al.* 2000; Naiman *et al.* 2005; Schachtschneider 2009) and it is likely that all three species were able to do so at the study sites. Thus, while it is acknowledged that further study incorporating more species and other water sources, such as subsurface flow, groundwater fluctuations and soil moisture are needed, this result is potentially highly significant in the context of environmental flow implementation in the Western Cape, since demand for water is highest during the dry season, when rainfall and river flows are low (Brown *et al.* 2006). Immense pressure is placed on summer base flows due to abstraction of water from rivers and tributaries that can leave standing pools disconnected and whole tributary reaches dry (Brown *et al.* 2006; Le Roux 2013). Riparian vegetation provides food for aquatic biota (King 1981) and contributes to bank stability (Thorne 1990) so maintaining dry season flows for the sustenance of marginal riparian communities has been a strong motivator toward environmental water requirement allocations (Naiman *et al.* 2000; Richter *et al.* 2006; Naiman *et al.* 2008). If it transpires that the survival of wet and dry bank trees is not dependent on summer flows, it could change the notion that these are essential to maintain riverine ecosystem structure (King *et al.* 2008). Successful recruitment of riparian seedlings and the establishment of saplings is one of the main characteristics that determine a healthy riparian vegetation community (Kleynhans *et al.* 2007). *S. mucronata* relies on summer base flows to disperse seed and, to maintain moisture levels for seedling establishment (Guilloy *et al.* 2011), which means that the extent to which over abstraction of summer flows hinders the health of *S. mucronata* populations is related to its dependence on seed-driven recruitment. The differences demonstrated by these three species also suggest that riparian species may adopt more than one reproductive or persistence strategy in response to the varied flow regime.

In conclusion, all the trees revealed synchronicity with the flow regime according to the predictions made in relation to their position in the wet or dry bank. The two dry bank

species differed from each other in the mode of adaptation, and both were different from *S. mucronata* in ways that matched the predictions associated with the hydraulics of the two bank positions (Chapter 4). Seeds were not released over a longer period than in more hydrologically-stable systems but the pattern differed between species, and again the two dry bank occupants revealed different strategies. The mixed population structure of Fynbos Riparian Vegetation (Chapter 3) could result from differences in inter-annual recruitment success between species. The Fynbos Biome is extraordinarily species rich and the terrestrial flora (Kruger and Taylor 1980) are characterised in particular by a high species turnover between basins that is linked to geographic variation across climatic gradients (Cowling *et al.* 1992). Geographic variation in species composition between river basins is also characteristic of Fynbos riparian communities Sieben *et al.* (2009) as was the lateral gradients described in Chapters 3 and 4.

6 Using a reference condition of lateral zones to assess recovery of Fynbos Riparian Vegetation

Karen Esler, Cate Brown and Jackie King are co-authors as each contributed towards the concepts therein and reviewed the manuscript.

6.1 Introduction

Biological invasions represent the second largest threat (after habitat destruction) to global biodiversity (Wilcove *et al.* 1998). Ecotones, such as riparian areas, are particularly sensitive to environmental change and invasion (Naiman and Decamps 1997; Tickner *et al.* 2001). Riparian areas are vulnerable to anthropogenic disturbance (Richardson *et al.* 2007), which results from impounding and diversion of water, abstraction of water from alluvial aquifers, overgrazing by livestock, removal of trees for building and firewood, clearing of land for cultivation, mining, roads, recreational use and fire (Naiman *et al.* 2005). This vulnerability is heightened in semi-arid regions at least partly due to water being available in an otherwise dry landscape (Dye *et al.* 2001), but also because violent floods create patches of open sediment ideal for germination of hydrochorous seed (Knight 1985, Versfeld *et al.* 1998) – in particular invasive seed. In the process, indigenous vegetation communities are displaced and invasive species introduced. As a result many riparian areas require sustained management to prevent re-invasion (Richardson *et al.* 1997).

The impacts of woody invasives on riparian areas include: suppression and replacement of indigenous vegetation (Holmes *et al.* 2005); reductions in species richness and indigenous tree recruitment (Galatowitsch and Richardson 2005); reduced runoff into rivers (Dye 2006) and increased sediment deposition as a result of flow resistance by dense woody stands (Rowntree 1991); channel widening in headwater streams as a result of erosion, and deepening and narrowing of lowland rivers as sediment is trapped and stored (Rowntree 1991); changes in leaf litter fall (King 1981); and increased flammability and heat generated by fires, leading to 'heat scars' and the death of indigenous seeds in surface soil layers (Cilliers 2002). Richardson and van Wilgen (2004) also discuss anecdotal evidence of alterations in the provision and delivery of riparian/fluvial goods and services other than water:

- increased amount and diversity of seed resources for frugivorous birds and decreased availability of food supplies for insectivorous bird species;
- increased biomass and woody fuel loads, leading to increased susceptibility to fire and soil erosion, and;
- increased runoff in basins devoid of topsoil and groundcover causing increased severity of flooding, damage to property and siltation of reservoirs.

One of the most contentious issues in South Africa is water use by woody invasives that are said to have considerably higher rates of transpiration (Dye *et al.* 2001), and thus use more water, than their indigenous counterparts (Dye and Poulter 1995; Versfeld *et al.* 1998). Different studies provide a range of estimates for reductions in river flow and thus water yields from basins based upon the degree to which natural vegetation guilds have been displaced. For example, reduction in river flows is estimated at 6-22% if indigenous forests are replaced by invasive trees, depending upon the species of invasive (Le Maitre *et al.* 2004), and up to 50% where grassland is replaced by invasive trees (van Wilgen *et al.* 2012). Rebelo (2012) estimated that clearing invasives from wetlands in the upper Kromme River and reinstating natural hydrological functioning of these wetlands would result in a 30% increase in mean annual runoff downstream. In South Africa, the impact of woody invasives on water availability was considered so severe that the Working for Water (WfW) programme was launched in 1998 (Van Wilgen *et al.* 1998) to clear invaded river basins. Fifteen years on, it is still uncertain whether or not the predictions of significant benefits arising from control are warranted or whether the spread of invasives can be curbed (van Wilgen 2004).

Woody invasives fundamentally alter riverine processes through changes in canopy structure and the abundance and variety of taxa (Holmes *et al*. 2005). Once they appear in riparian areas, they exploit invasion windows created by flood events and anthropogenic disturbance to spread (Levine and Stromberg 2001). Positive feedback mechanisms may promote further establishment via habitat alteration and increased propagule pressure (Richardson *et al.* 2007), as shown for *Sesbania punicea* in South Africa (Hoffmann and Moran 1988). Essentially, a mixed plant community may be replaced by a woody monoculture, which affects the flow and availability of nutrient and trophic resources, and access to physical resources such as light, sediment, space or water (Richardson *et al.* 2007). The extent of the change depends on the invasive species and density of invasion (Richardson *et al.* 2007), its consumptive use of water (Ticker *et al.* 2001) and its effect on hydraulic resistance (or roughness) in the riparian area (Darby 1999). In this regard, some particularly aggressive invasives are considered to be transformers or ecosystem engineers (Crooks 2002) since changes to riverine vegetation can effect changes to river channel structure (Naiman *et al.* 2005) and aquatic habitat. Grass and tree species influence river bank structure in different ways. For example, grasses and other shallow-rooted herbaceous perennials offer good protection against surface scour but no defences against mass bank failure (Micheli and Kirncher 2002), while trees are deeply rooted, which increases protection against mass bank failure (Thorne 1990). Thus, a well vegetated river bank with a variety and combination of groundcovers and trees is better protected against a range of hydraulic conditions than by one with a monoculture of either groundcovers or trees.

Most studies on the impacts of invasion or recovery after clearing are conducted at scales of 50 m^2 or larger (Prins *et al*. 2005; Blanchard and Holmes 2008; Vosse *et al.* 2008; Jacobs *et al*. 2013). In narrow riparian areas, such as those located in headwater streams which may be only 5 m in width, a 50 m^2 sample plot may include all the lateral zones of the riparian area, not differentiating them. Even further down the river's longitudinal profile, where the riparian zone is wider, several zones could be covered by a single plot. In order to investigate the implications of variable flow between (Chapter 4), and the presence of different functional types in (Chapter 5), lateral vegetation zones on the processes of invasion and recovery, it is necessary to work at a finer scale.

The re-establishment of an indigenous community subsequent to clearing of invasives may follow a number of trajectories toward alternate stable states (Schröder *et al*. 2005) depending on the density of invasion, the standing stocks of indigenous species and the clearing methods used (Holmes *et al.* 2005; Milton 1980; Richardson and van Wilgen 1986; Pieterse and Cairns 1986, 1988; Versfeld *et al.* 1988; Richardson *et al.* 1989; Musil and Midgley 1990; Pieterse 1997; Van den Berckt 2001). For example, Reinecke *et al.* (2008) described a proliferation of nitrophilic grasses at sites cleared of *Acacia saligna*, but at nearby sites cleared of *Pinus pinaster,* recovery was towards a mixed shrubland.

The impacts of woody invasives may be better understood if compared to a reference condition where they are contextualised within the same lateral zones as the indigenous vegetation (Chapter 3), based on variable flows between zones (Chapter 4) where functional differences between zones have been demonstrated (Chapter 5). It would useful to know to what extent the presence of an invasive species disrupts the structure and species composition of a riparian community, which are linked to the unique river signatures described for the reference sites (see Section 3.4). River signatures have been described on the basis of basin-level differences in relative abundance between species rather than differences in the species themselves. These patterns are explored at a basin-scale. It would also be useful to know whether the four zones are equally susceptible to invasion or whether the lower dynamic, being an area of active recruitment, might be a favoured location for the recruitment. Similarly, which indigenous species are able to persist and whether this differs between zones may be useful when considering restoration strategies.

In this chapter the key question (Figure 1.1) was, "Is a framework of lateral zones useful to assess recovery after clearing invasives from Fynbos Riparian Vegetation?" This was incorporated into two hypotheses:

- Sites invaded by the same species are more similar to one another than to reference sites and/or sites invaded by other species in the same river basin.
- Invasives do not establish equally well in each lateral zone.

6.2 Methods

6.2.1 Data collection

Data were collected from 16 headwater streams; five invaded and 11 cleared (Table 6.1). The same methods of biophysical data collection used at the reference sites (Chapter 3) were used at the cleared and invaded sites (Table 6.2). There was one group of invaded sites, those by the Australian black wattle *Acacia mearnsii,* but at two of the sites there were some isolated individuals of the Australian blackwood *A. melanoxylon* and *Eucalyptus* trees. For the purposes of this chapter we restricted our focus to the dominant invasive *A. mearnsii.* There were no sites invaded by *Pinus* included in the sample set. All cleared sites were similar in that they were treated with fell/burn, were subject to regular and successive follow-up clearing and were located in headwater streams where the natural vegetation was Fynbos Riparian Vegetation. They differed in the time since being cleared, the invading species present and their location by river basin. The 16 reference sites from Chapter 3 were used to compile a comparable reference condition by standardising their data and then combining them into one data set for analysis. The occurrence of each species at the invaded and disturbed sites is shown in Appendix Table 8.3 and habitat characteristics are described in Appendix Table 8.4 (nomenclature follows Goldblatt and Manning 2000).

6.2.2 Data analysis

The same methods of data analysis used in Chapter 3 were used to compare the relationships between the reference, cleared and invaded sites at a river scale. Additional analyses are reported on below.

Table 6.1 Invaded and cleared study sites in Western Cape headwater streams. mAsl = metres above sea level. Zones as per Rowntree *et al.* (2000), Table 2.1. c = cleared and i = invaded.

Basin	River	Code	Zone	Gradient	Altitude (mAsl)	Co-ordinates
Olifants	Rondegat	cR5	Transitional	0.025	335	S 32.341333°, E 19.021167°
		iR6	Transitional	0.025	333	S 32.335050°, E 19.020183°
Breede	Witte	iW3	Upper Foothills	0.027	258	S 33.555916°, E 19.152083°
		cW4	Upper Foothills	0.027	253	S 33.555733°, E 19.152300°
	Molenaars	cM1	Upper Foothills	0.012	406	S 33.723950°, E 19.147717°
		cM2	Upper Foothills	0.012	375	S 33.723117°, E 19.179367°
		cM3	Upper Foothills	0.006	282	S 33.709667°, E 19.197467°
		iM4	Upper Foothills	0.006	258	S 33.696217°, E 19.214883°
Berg	Assegaaibos	cA1	Transitional	0.024	275	S 33.967267°, E 19.081033°
		iA2	Transitional	0.024	295	S 33.967633°, E 19.079617°
		cA3	Transitional	0.024	295	S 33.967633°, E 19.079617°
	Sir Lowry's Pass	c$1	Mountain Stream	0.087	315	S 34.093817°, E 18.946683°
		c$2	Mountain Stream	0.067	293	S 34.094767°, E 18.944900°
		i$3	Transitional	0.042	189	S 34.103033°, E 18.931800°
	Silvermine	cS1	Mountain Stream	0.050	305	S 34.088500°, E 18.419000°
		cS2	Transitional	0.035	114	S 34.104267°, E 18.420883°

Table 6.2 History of disturbed sites. Site codes as per Table 6.1. i = invaded and c = cleared. Cleared is year of first clearing. Fire = wild fire.

Site	Invasion	Cleared	Method	Fire	Sampled	Invasive species present
cR5	<25%	1998	Fell/burn	-	2005	*Acacia mearnsii, A. melanoxylon, Eucalyptus sp.*
iR6	>75%	-	-	-	2005	*Acacia mearnsii, A. melanoxylon, Eucalyptus sp.*
iW3	>75%	-	-	-	2004	*Acacia mearnsii, A. melanoxylon*
cW4	25-50%	1997	Fell/burn	2001	2004	*Acacia mearnsii, A. melanoxylon*
cM1	<25%	1994	Fell/burn	-	2004	*Acacia mearnsii*
cM2	<25%	Pre-1988[18]	-	-	2004	*Acacia mearnsii*
cM3	<25%	1997	Fell/burn	-	2004	*Acacia mearnsii*
iM4	>75%	-		-	2004	*Acacia mearnsii*
cA1	<25%	2000	Fell/burn	-	2004	*Pinus radiata*
cA2	<25%	2002	Fell/burn	-	2004	*Pinus radiata*
cA3	<25%	2004	Fell/burn	-	2005	*Pinus radiata*
c$1	<25%	1992	Fell/burn	-	2005	*Pinus pinaster, A. longifolia, A. saligna*
c$2	<25%	2002	Fell/burn	-	2005	*Pinus pinaster, A. longifolia, A. saligna,*
i$3	>75%	-	-	-	2005	*Eucalyptus leucoxylon, Acacia mearnsii*
cS2	<25%	2000	Fell/burn	2000	2005	*Acacia saligna, A. longifolia*
cS1	<25%	2000	Fell/burn	2000	2005	*Pinus pinaster*

6.2.2.1 Comparison between sites

Taxa responsible for group separation were described first by growth form (Table 3.2) and then at the species level. Species-cover abundances were standardised across sites and then combined according to growth form. The mean abundance and standard error for each growth form in the five basins were calculated and differences between groups tested using one-way ANOVAs (StatSoft 2013). Ten adjacent sample plots were chosen at random from the sample grid and two measures of species richness (50 m^2), Shannon Weiner equitability (H) and Pielou's relative diversity (J) coefficient (Zar 1996), were calculated and compared using t-tests (StatSoft 2013).

6.2.2.2 Comparison of lateral zones

Samples from invaded and cleared groups were assigned to different lateral zones using the rules from Chapter 3. The data were standardised prior to calculation of ranked frequency of occurrence and average abundance, per species in sample groups. Species frequency of occurrence and abundance data were summarised for lateral zones at reference, invaded and cleared sites and compared. The average species richness (5 m^2) per lateral zone within river groups was compared using t-tests (StatSoft 2013).

[18] Site cM2 was said to be pristine by Boucher (1988) but grouped with cleared sites, not with reference sites. On this basis I have assumed it was invaded at some stage prior to this before being cleared. At the time of sampling some invasive recruitment of *Acacia mearnsii* and *Sesbania punicea* were recorded.

6.3 Results

6.3.1 Basin scale patterns

Cluster analysis and MDS of reference, invaded and cleared sites revealed five groups (Figure 6.1). A single site invaded by *Eucalyptus leucoxylon* (i$3) was an outlier, due to being depauperate of plant species, in term of density and abundance and was not considered further. The five groups (Table 6.3) were Group 1, comprised of 16 reference sites; Group 2, comprised of three sites on the Molenaars River, two cleared of *Acacia mearnsii* and one site described to be a reference site by Boucher (1988) but that grouped here with the cleared sites; Group 3, comprised four *A. mearnsii* sites, three invaded on the Rondegat, Witte and Molenaars Rivers and one cleared site on the Witte River; Group 4, comprised three sites cleared of *Pinus radiata* on the Assegaaibos River, and; Group 5, comprised of four cleared sites, two on the Silvermine River cleared of *Pinus pinaster* and *Acacia saligna* respectively, and two on the Sir Lowry's Pass River cleared of *Pinus pinaster.*

The global R^2 test of group similarity (R^2 = 0.796) and the paired-wise comparisons between river groups (1-5) based upon species abundances showed that the five groups differed from one another (Table 6.4) and this was largely a product of species composition (R^2 = 0.753) but age since clearing was also a factor (R^2 = 0.64).

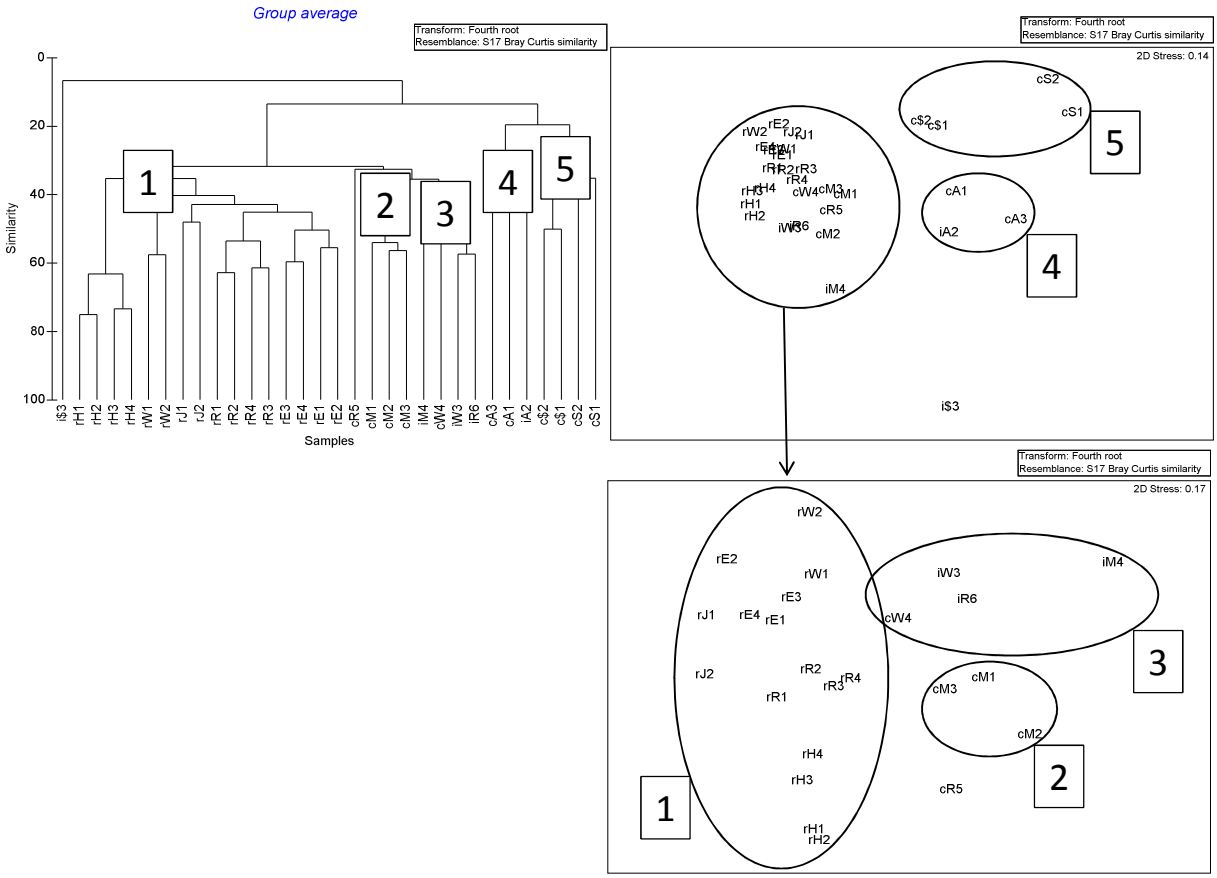

Figure 6.1 **CLUSTER and MDS ordination of Bray Curtis similarity between species composition of sites. Site codes as per Table 6.1. Sample plot codes as per Figure 3.1.**

Table 6.3 Historical condition of sites in groups 1-5 of Figure 6.1. Site codes as per Table 6.1.

Group	Sites	Condition	Time since clearing (if applicable)	Invasive species
1	rR1-4 rH1-4 rE1-4 rJ1-2 rW1-2	Reference	N/a	N/a
2	cM1 cM2 cM3	Cleared Cleared Cleared	11 ? 7	*Acacia mearnsii* *Acacia mearnsii* *Acacia mearnsii*
3	iM4 iR6 iW3 cW4	Invaded Invaded Invaded Cleared	N/a N/a N/a 7 years	*Acacia mearnsii* *Acacia mearnsii* *Acacia mearnsii* *Acacia mearnsii*
4	cA1 cA2 cA3	Cleared Cleared Cleared	4 2 1	*Pinus radiata* *Pinus radiata* *Pinus radiata*
5	cS1 cS2 c$1 c$2	Cleared Cleared Cleared Cleared	5 5 3 13	*Pinus pinaster* *Acacia saligna* *Pinus pinaster* *Pinus pinaster*

Table 6.4 R^2 values for pairwise tests of differences between groups 1-5 at a 5% level (*).

Group	2	3	4	5
1, reference	0.612*	0.590*	0.998*	0.993*
2, Molenaars River		0.549*	0.926	0.852*
3, Molenaars/Witte/Rondegat Rivers			0.959*	0.950*
4, Assegaaibos River				0.815*
5, Silvermine/Sir Lowry's Pass Rivers				

The invaded groups (Groups 2-5) were more obviously separated according to invasive species than by age since clearing commenced. Groups 2 and 3, Berg and Breede River basins, which were all sites invaded by, or cleared of, *Acacia mearnsii,* grouped most closely with their corresponding reference sites. Group 2 comprised of two sites that had been cleared for more than seven years (Table 6.3), while Group 3 comprised one site cleared for seven years but also burnt by a wild fire three years prior to sampling (Table 6.2). Groups 4 and 5 comprised sites in the Berg River cleared predominantly of two *Pinus spp.* but also other invasives, such as *Acacia longifolia and A. saligna* (Table 6.2), and were well separated from Groups 1-3. Group 4 comprised three sites cleared of *Pinus radiata* between one and four years prior to sampling while Group 5 consisted of three sites cleared of *Pinus pinaster* between three and 13 years prior to sampling, and a third site on the Silvermine cleared of *Acacia saligna* five years prior to sampling.

To some extent the pattern shown was driven by the invasive species present, but there were also indications that age since first clearing, providing regular follow-up clearing had taken place and that the same method of clearing was used, was a factor. The highest species richness (50 m^2) was recorded in Group 4, the most recently cleared sites, while the lowest values were recorded for the invaded sites of group 3 (Table 6.5). Species abundances were less evenly distributed (H, Shannon-Weiner's function; Zar 1996) at invaded sites (Group 3) than at cleared sites (Groups 2, 4 and 5), when compared to the reference condition. The invaded sites of Group 3 and those most recently cleared, Group 4,

both had lower relative diversity scores (J, Pielou's coefficient; Zar 1996), which indicated a weaker numerical contribution by dominant species toward group identity.

Table 6.5 **Mean (± SD) species richness (Sp./50 m^2) between groups. Shannon-Weiner function (equitability: H) and Pielou's relative diversity (J). * = p< 5%. n = number of sites.**

	Sp./50 m²	H	J
1 Reference	22.67 ± 5.80	2.38 ± 0.23	0.80 ± 0.06
2 Molenaars (n=3)	27.67 ± 3.51	***2.69 ± 0.23**	0.78 ± 0.02
3 Molenaars/Witte/Rondegat (n=4)	***11.60 ± 5.80**	***1.65 ± 0.99**	***0.58 ± 0.31**
4 Assegaaibos (n=3)	***37.33 ± 9.07**	***2.95 ± 0.86**	***0.76 ± 0.09**
5 Silvermine/Sir Lowry's Pass (n=4)	28.75 ± 8.81	***2.76 ± 0.28**	0.82 ± 0.58

The distribution of growth forms between reference, invaded and cleared sites differed (Table 6.6). When compared to the reference group, the abundance of small trees at all invaded and cleared sites was lower. The cleared sites on the Assegaaibos River (Group 4) had a higher abundance of rushes and fewer small trees while the cleared sites on the Sir Lowry's Pass and Silvermine Rivers (Group 5) had a greater proportion of shrublets than the other sites. Overall the Molenaars River group stood out with higher abundances in six of 11 growth forms: forbs, geophytes, rushes, sedges, grasses and shrubs were all higher in abundance than at reference sites.

Table 6.6 **The mean, and standard deviation (SD) about, percentage cover of each growth forms in river groups. Growth form categories as per Table 3.2. (n) = number of sites in each group. * = p < 5%. SD = standard deviation.**

Growth form	Forb	Geophyte	Rhizome	Rush	Sedge	Grass	Restio	Shrublet	Shrub	Small tree	Large tree
1 Reference											
Mean (n=16)	1.41	0.00	10.96	0.42	3.14	10.52	9.92	1.27	9.57	49.50	13.18
SD	3.21	0.00	16.06	0.91	3.34	11.30	9.14	1.85	8.02	23.61	23.00
2 Molenaars											
Mean (n=3)	**9.00***	**0.13***	9.17	**15.27***	**8.39***	**17.41***	10.06	**13.20***	10.95	**18.86***	1.70
SD	**13.83**	**0.13**	9.08	**24.01**	**5.02**	**15.38**	8.96	**19.94***	3.71	**16.27**	1.39
3 Molenaars/Witte/Rondegat											
Mean (n=4)	3.73	0.00	8.06	1.84	11.41	9.59	2.53	3.92	10.48	**20.27***	15.42
SD	4.48	0.00	8.45	2.02	18.04	12.08	1.64	4.55	14.08	**22.49**	23.66
4 Assegaaibos (n=3)											
Mean (n=3)	3.73	0.03	4.33	**8.40***	6.43	8.03	5.77	3.07	3.66	**12.14***	26.98
SD	2.96	0.05	1.66	**11.62**	4.42	5.56	1.31	2.72	2.80	**8.07**	20.99
5 Silvermine/Sir Lowry's Pass											
Mean (n=5)	0.03	0.00	3.85	0.02	2.07	6.64	7.47	**4.90***	5.15	32.23	5.57
SD	0.06	0.00	2.60	0.04	1.49	6.62	3.10	**3.25**	3.01	17.10	4.92

SIMPER analyses listed typical species for each group (Table 6.7). The rush, *Juncus lomatophyllus,* and the sedge, *Isolepis prolifera,* were more abundant at sites forming Group 2. Three small indigenous trees, *Metrosideros angustifolia, Brabejum stellatifolium* and *Brachylaena neriifolia,* persisted under invasion and through clearing of *Acacia mearnsii* in the Berg and Breede River basins of Group 3. At severely invaded sites (such as iW3, iR6

and iM4) the tree *Brabejum stellatifolium* was present and the shrub *Diospyros glabra* was relatively common. The rush, *Juncus capensis,* was common at Group 4 along with some other *Juncus* spp., while the shrublet, *Helichrysum cymosum,* was common at Group 5 sites.

Table 6.7 Typical species of each group. Sim = similarity coefficient. J = sapling, T = tree and S = seedling. Species are listed in decreasing order of importance.

Group	Sim. (%)	Species
1 Reference	42	*Metrosideros angustifolia J, Elegia capensis, Metrosideros angustifolia T, Calopsis paniculata, Morella serrata T, Brachylaena neriifolia J, Diospyros glabra, Morella serrata J* and *Brabejum stellatifolium T&J.*
2 Molenaars	55	*Juncus lomatophyllus, Isolepis prolifera, Metrosideros angustifolia S, Persicaria lapathifolia, Brabejum stellatifolium T* and *Prionium serratum.*
3 Molenaars/Witte/Rondegat	42	*Prionium serratum, Metrosideros angustifolia J, Acacia mearnsii J, Acacia mearnsii T, Metrosideros angustifolia T, Diospyros glabra, Brabejum stellatifolium T&J, Brachylaena neriifolia T&J and Metrosideros angustifolia S.*
4 Assegaaibos	35	*Metrosideros angustifolia J, Stoebe cinerea, Taraxacum officinale, Halleria elliptica, Paspalum urvillei, Juncus capensis, Histiopteris incisa* and *Conyza canadensis.*
5 Silvermine/Sir Lowry's Pass	32	*Histiopteris incisa, Juncus capensis, Berzelia lanuginosa, Isolepis prolifera, Ehrharta setacea, Helichrysum cymosum* and *Taraxacum officinale.*

The SIMPER routine also listed discriminant (Table 6.8) species for each group. In three of the four comparisons, the restio *Elegia capensis* was the strongest discriminator for the reference Group (1), second only to saplings of *Metrosideros angustifolia* when compared with Group 5. In contrast, Group 2 was most strongly characterised by the disturbance-triggered forb *Persicaria lapathifolia* and the terrestrial riparian grasses *Eragrostis curvula* and *Paspalum urvillei,* respectively, along with saplings and seedlings of both *Acacia mearnsii* and *Salix mucronata*.

The sole discriminants for Group 3 were trees and saplings of *Acacia mearnsii.* Group 4 was strongly characterised by species common to invaded landscapes, such as the weedy forb, *Taraxacum officinale,* and the grass, *Paspalum urvillei,* along with the terrestrial or forest-edge shrubs, *Halleria elliptica* and *Stoebe cinerea.* The indigenous rushes *Juncus lomatophyllus, J. capensis, J. effusus* and *J. exsertus,* were also characteristic. Finally, Group 5 was similar to Group 4 as it was characterised by non-riparian species such as the herbaceous perennial, *Histiopteris incisa,* the grass *Ehrharta setacea,* known to flourish in cleared landscapes (Reinecke *et al.* 2008), the weedy forb *Taraxacum officinale,* the shrub *Berzelia lanuginosa,* common on seeps, and the shrublet *Helichrysum cymosum.*

The sites invaded by *A. mearnsii* represent one end of the spectrum, being species poor and lacking a dominant taxon. The sites most recently cleared of *Pinus* spp. represent the other being most species rich but also lacking a dominant taxon. The sites that have been kept clear for longer appeared to gravitate back toward a distribution of taxa comparable to the reference sites but with two notable exceptions. The small tree guild was largely absent from all invaded or cleared groups regardless of invasive species. Secondly, the three cleared sites all were characterised by one over-abundant guild; grasses were more abundant at sites cleared of *A. mearnsii*, rushes were more abundant at sites cleared of *P. radiata* on the Assegaaibos River and shrublets were more abundant at sites cleared of *P. pinaster* and *A. saligna* on the Silvermine River.

Table 6.8 **Discriminant species between groups. J = sapling, T = tree. Bolded species are incidental and underlined are invasive. Diss/SD = dissimilarity coefficient/standard deviation.**

1 Reference dissimilarity = 68%	Diss/SD	2 Molenaars	Diss/SD
Elegia capensis	*4.40*	*Persicaria lapathifolia*	*6.08*
Juncus lomatophyllus	*4.26*	***Eragrostis curvula***	*4.51*
Juncus effusus	*2.80*	*Paspalum urvillei*	*3.89*
		Salix mucronata J	*3.04*
		Acacia mearnsii S	*3.01*
		Salix mucronata S	*2.29*
		Acacia mearnsii J	*2.19*
1 Reference dissimilarity = 69%		3 Molenaars/Witte/Rondegat	
Elegia capensis	*2.24*	*Acacia mearnsii T*	*2.25*
		Acacia mearnsii J	*2.17*
1 Reference dissimilarity = 87 %		4 Assegaaibos	
Elegia capensis	4.64	*Taraxacum officinale*	8.14
Histiopteris incisa	4.52	***Paspalum urvillei***	5.07
Brachylaena neriifolia J	2.96	*Juncus lomatophyllus*	4.64
Morella serrata J	2.89	*Juncus effusus*	3.28
Morella serrata T	2.37	***Juncus capensis***	3.05
Brachylaena neriifolia T	2.31	***Halleria elliptica***	2.58
		Juncus exsertus	2.47
		Stoebe cinerea	2.33
		Acacia longifolia J	2.29
1 Reference dissimilarity = 88%		5 Silvermine/Sir Lowry's Pass	
Metrosideros angustifolia J,	*4.89*	***Histiopteris incisa***	*5.59*
Metrosideros angustifolia T	*4.35*	***Ehrharta setacea***	*4.41*
Elegia capensis	*4.49*	***Juncus capensis***	*4.16*
Morella serrata T	*2.34*	*Taraxacum officinale*	*2.56*
Morella serrata J	*2.46*	*Berzelia lanuginosa*	*2.43*
		Helichrysum cymosum	*2.25*

6.3.2 Changes in lateral plant distribution

Species richness was generally similar between lateral zones across groups even though species composition differed. When compared to the reference condition, fewer species were recorded in the upper zones of the *A. mearnsii* sites, both at the cleared Group 2 and invaded Group 3, where the species richness of the lower zone was also lower (Table 6.9).

Table 6.9 **Mean species richness (5 m^2) (± Standard Deviation) of lateral zones per group. Mar. = marginal, L.D. = lower dynamic, Low. = lower and Upp. = upper. n = number of sample plots.**

	Mar.	L.D	Low.	Upp.
1 Reference	6.1 ± 4.2 (n=85)	9.1 ± 5.9 (n=121)	8.8 ± 2.9 (n=250)	19.9 ± 7.9 (n=128)
2 Molenaars	2.9 ± 2.0 (n=4)	9.2 ± 4.6 (n=12)	5.7 ± 2.0 (n=55)	**3.1 ± 1.4* (n=17)**
3 Molenaars/Witte/Rondegat	4.5 ± 3.1 (n=24)	4.7 ± 4.3 (n=27)	**3.1 ± 1.4* (n=179)**	**3.4 ± 0.0* (n=21)**
4 Assegaaibos	4.5 ± 4.5 (n=8)	7.2 ± 1.5 (n=12)	11.7 ± 5.0 (n=100)	(n=0)
5 Silvermine/Sir Lowry's Pass	5.4 ± 3.4 (n=14)	9.3 ± 4.9 (n=14)	9.2 ± 1.6 (n=72)	7.2 ± 1.1 (n=72)

Calopsis paniculata and *Erica caffra* were common occupants in the marginal zone of Group 1, but were absent from the invaded and cleared sites (Table 6.10). The sedge, *Isolepis prolifera,* occurred more frequently and in greater abundance at cleared sites than at reference sites. This sedge, together with the rush, *Juncus lomatophyllus,* was also common at cleared sites in Groups 4 and 5. Palmiet, *Prionium serratum,* a well-known inhabitant of

Fynbos rivers, occurred frequently at the invaded sites in Group 3, but not at the others. Small trees were recruiting into the marginal zone at Groups 1 and 2 whereas herbaceous species dominated this zone in Groups 4 and 5.

Table 6.10 Frequency of occurrence (F) and standardised average abundance (% cover) of marginal zone dominants. T = tree and S = seedling.

1 Reference	F (%)	% cover	Group	F (%)	% cover.
			2. Molenaars		
			Isolepis prolifera	99	81
			Freylinia lanceolata T&S	50	14
			Salix mucronata T&S	25	03
			3. Molenaars/Witte/Rondegat		
Isolepis prolifera	27	16	*Prionium serratum*	63	07
Calopsis paniculata	20	16	*Metrosideros angustifolia T*	38	09
Prionium serratum	16	08	*Cannamois virgata*	33	13
Metrosideros angustifolia S	15	02	4. Assegaaibos		
Erica caffra	12	09	*Isolepis prolifera*	75	43
Salix mucronata J	12	04	*Juncus lomatophyllus*	75	24
			Taraxacum officinale	63	06
			5. Silvermine/Sir Lowry's Pass		
			Isolepis prolifera	79	18
			Juncus capensis	64	09
			Taraxacum officinale	36	03

Calopsis paniculata and *Elegia capensis,* two common riparian restios, were prominent in the lower dynamic zones of Groups 1 and 2, while herbaceous species or woody invasives were common to other groups (Table 6.11). Small trees and their saplings were common in Groups 1-3, while invasive trees were also present, along with their saplings, in the lower dynamic zones of Group 3.

Table 6.11 Frequency of occurrence (F) and standardised average abundance (% cover) of lower dynamic dominants. T = tree, S = seedling and J = sapling.

1 Reference	F (%)	% cover	Group	F (%)	% cover.
			2. Molenaars		
			Isolepis prolifera	75	38
			Pennisetum macrourum	67	19
			Salix mucronata T&S	58	05
Calopsis paniculata	28	11	3. Molenaars/Witte/Rondegat		
Panicum schinzii	17	12	*Acacia mearnsii T&J*	63	41
Morella serrata T	17	01	*Metrosideros angustifolia T&J*	56	21
Metrosideros angustifolia T	16	14	*Brabejum stellatifolium T&J*	41	13
Elegia capensis	15	05	4. Assegaaibos		
Morella serrata J	13	08	*Isolepis prolifera*	83	24
Isolepis prolifera	12	04	*Juncus lomatophyllus*	67	27
Morella serrata S	11	01	*Taraxacum officinale*	67	06
Metrosideros angustifolia S	10	01	5. Silvermine/Sir Lowry's Pass		
			Berzelia lanuginosa	79	11
			Carpha glomerata	57	06
			Isolepis prolifera	50	08

Elegia capensis occurred less frequently at, or was missing from, the lower zone at the invaded sites in Group 3 (Table 6.12). The lower zone of Groups 1 and 2 were most similar to each other, and were distinguished from the other groups by the presence of the tree *Metrosideros angustifolia.* The tree *Brabejum stellatifolium* was present at invaded sites in

Group 3 along with invasive trees that were also present as saplings but no indigenous small trees were present in Groups 4 and 5.

Table 6.12 Frequency of occurrence (F) and standardised average abundance (% cover) of lower zone dominants. T = tree and J = sapling.

1 Reference	F (%)	% cover	Group	F (%)	% cover.
			2. Molenaars		
			Metrosideros angustifolia T&J	60	10
			Brabejum stellatifolium T&J	44	17
			Calopsis paniculata	35	05
			3. Molenaars/Witte/Rondegat		
			Acacia mearnsii T&J	27	40
Pteridium aquilinum	12	13	*Brabejum stellatifolium T&J*	22	20
Elegia capensis	12	13	*Prionium serratum*	04	09
Metrosideros angustifolia T	12	16	4. Assegaaibos		
Brabejum stellatifolium T	12	10	*Paspalum urvillei*	30	10
			Taraxacum officinale	25	04
			Virgilia oroboides J	22	06
			5. Silvermine/Sir Lowry's Pass		
			Virgilia oroboides T&J	49	20
			Taraxacum officinale	42	06
			Briza maxima	39	09

Trees dominated the upper zones in Group 1 but were uncommon at invaded or cleared sites. The upper zones of the invaded sites were also less species rich (Table 6.9) than those in Group 1. The shrub *Diospyros glabra* was a common inhabitant of the upper zone in Groups 2 and 3 along with the trees *Metrosideros angustifolia* and *Brabejum stellatifolium.* There was no upper zone in Group 4 and that in Group 5 was dominated by herbaceous species (Table 6.13).

Table 6.13 Frequency of occurrence (F) and standardised average abundance (% cover) of upper zone dominants. T = tree and J = sapling.

1 Reference	F (%)	% cover	Group	F (%)	% cover.
			2. Molenaars		
			Pteridium aquilinum	99	46
			Diospyros glabra	41	14
			Brabejum stellatifolium T&J	29	28
			3. Molenaars/Witte/Rondegat		
Asparagus scandens	16	05	*Acacia mearnsii T*	90	13
Kiggelaria africana T	15	08	*Metrosideros angustifolia T*	86	40
Juncus effusus	11	09	*Diospyros glabra*	81	16
Virgilia oroboides T	11	02			
Cunonia capensis T	10	05	4. Assegaaibos		
			-	-	-
			5. Silvermine/Sir Lowry's Pass		
			Carpha glomerata	36	07
			Helichrysum cymosum	35	07
			Ehrharta setacea	25	06

There was little to no persistent recruitment of any invasive species, *Pinus* or *Acacia* spp., at the cleared sites due to regular follow up clearing of recruiting individuals. The frequency of occurrence and abundance of the invasive *Acacia mearnsii* and its saplings at invaded sites (Group 3) differed between zones. There were no individuals in the marginal zone (Table 6.10) while saplings and trees comprised 41% of the cover in two out of three lower dynamic plots (Table 6.11). *Brabejum stellatifolium* and *Metrosideros angustifolia* co-occurred with

Acacia mearnsii one quarter to half of time respectively in lower zone plots respectively but at half the cover. *Acacia mearnsii* and *Metrosideros angustifolia* featured in a quarter of the upper zone plots but *A. mearnsii* was twice as abundant (Table 6.12). *Acacia mearnsii* trees were most frequently recorded in the upper zone at invaded sites but were most abundant in the lower dynamic (Table 6.13).

The lower and upper zones invaded by, and cleared of, *A. mearnsii* were most species poor and were dominated by one or a few species. All the other zones at the *Pinus* and *A. mearnsii* sites were comparable in terms of species richness but the abundances of some of the indigenous species varied beyond reference values, with more graminoids and fewer small trees and saplings.

6.4 Discussion

The structure of invaded riparian zones, and their trajectories of recovery after clearing, differed depending on the invasive species. However, these differences were more closely related to site history, particularly anthropogenic land use, than to the attributes of the invasive species.

Sites invaded by *Acacia mearnsii* grouped together regardless of river basin. Thus the invasive displaced the indigenous vegetation to such an extent that it overrode the river signatures described in Chapter 3. There were no invaded *Pinus* sites. The single site invaded by *Eucalyptus leucoxylon* also masked the river signature. It separated out from the rest as an outlier and had the poorest representation of remnant indigenous species. The data show that as invasives establish, the structure of the riparian vegetation community shifts away from one comprised of a diverse array of species and variety of growth forms to one dominated by the invader species, with a few remnant indigenous species. Once cleared, these sites recover back towards the reference condition but after 13 years there were still some characteristic species missing.

The recovery of sites cleared of *A. mearnsii* was more pronounced than that of sites cleared of *Pinus radiata* and *P. pinaster.* However, it was not possible to separate the effect of time since clearing from other influences such as invasive species; fire (both wild and as part of the clearing method; Cilliers *et al.* 2004); historical land management practices (Le Maitre *et al.* 2004) and river based signatures. Holmes *et al.* (2005) reported that recovery of fell/burn sites was protracted up to 5 years after clearing, a finding supported by Galatowitsch and Richardson (2005). Most cleared sites grouped first according to river basin and then according to invasive species cleared. The one exception to this was at the Silvermine River where the two sites grouped together despite one being cleared of *Pinus pinaster* and the other of *Acacia saligna.* This is probably because that Silvermine valley has been farmed since *ca.* 1820 and was the site of silver mining activities (Mr Len Sweet, pers. comm. 2001). This probably created the disturbed community characterised by a lack of small trees, presumably cleared for building material or firewood that persisted through the invasion and subsequently after clearing. Similarly, differences between the other sites with *A. mearnsii* and *Pinus* probably relate to the fact that the *A. mearnsii* sites were situated in wilderness areas while the *Pinus* sites were in forestry areas that had been subjected to site preparation, such as slash and burn (March 1978).

Using the rules based on bank shape described in Chapter 3, four zones were distinguished at each site, and used to compare zone characteristics of the invaded and cleared sites with the reference condition. There was some reservation about the use of these rules since invasives are known to effect changes to river channel morphology, especially the channel width:depth ratio (Rowntree 1991; Richardson *et al.* 2007) and sediment calibre of the river bank (Brown *et al.* 2004). Indeed, there was more coarse sand at the invaded sites than at the reference sites, and the sediments near the wetted edge were generally larger calibre, an

observation also made by Brown *et al.* (2004) beneath *Acacia mearnsii* stands. However, the rules provided a framework for understanding the sites in relation to reference sites (Chapter 3), hydraulic influences of river flow (Chapter 4) and functional differences (Chapter 5) that would otherwise not have been possible.

At the sites invaded by *A. mearnsii*, the zone delineations showed that invasion started in the lower dynamic zone, where adult and sapling *A. mearnsii* were most abundant. In un-invaded systems, the lower dynamic zones were the least densely vegetated of the four zones (Chapter 3), the most varied in terms of inundation duration and the frequency of inter- and intra-annual floods (Chapter 4), and were areas of active recruitment comprised mainly of recruiting seedlings and saplings (Chapter 5). Regular flooding facilitates gap creation for recruitment by removing competitors and also provides water and nutrients for germination and growth of seedlings (Richardson *et al.* 2007). As such, it makes sense that the lower dynamic was the zone exploited by *A. mearnsii*. It also explains why floods enhance the spread of invasives through riparian areas (Knight 1985; Levine and Stromberg 2001; Richardson *et al.* 2007).

The next most frequent occurrence of *A. mearnsii* was in the lower zone followed by the upper zone, suggesting that, once established in the lower dynamic zone, they spread up the banks, away from the water. Their success is attributable to the young age at which a sapling may first flower (12-14 months from germination, Richardson and Kluge 2008), heavy seed production and ability to form persistent seed banks of water impervious, hard-coated seeds, which remain viable for up to 37 years (Brown and Ko 1997). Heat from fire stimulates mass germination, but seeds also germinate as the seed coat breaks down naturally (Richardson and Kluge 2008). These seed banks hamper restoration efforts as the seeds occur up to 1 m deep in coarse sands deposited amongst the trees during floods (Brown *et al.* 2004).

Some indigenous species were able to persist at sites invaded by *A. mearnsii*. For example, the shrub *Prionium serratum* was highly abundant in the marginal zone but other characteristic restios, small trees and shrubs were absent. *P. serratum* is known to dominate erosive wet banks (Sieben and Reinecke 2008) and its proliferation at *A. mearnsii* sites supports the contention *A. mearnsii* invasions cause bank instability (Rowntree 1991). This also explains why no *A. mearnsii* trees or saplings were found in the marginal zone. Higher up the bank, *M. angustifolia* and *B. stellatifolium* were evenly-distributed across the lower dynamic and lower zones, whereas they were more abundant in the lower zone at reference sites. Other characteristic species of the lower dynamic zone, notably obligate riparian species such as the restios, *Calopsis paniculata* and *Elegia capensis,* the grass *Panicum schinzii,* and the tree, *Morella serrata,* were absent. This may relate to the presence of *A. mearnsii* trees resulting in reduced soil moisture (Dye and Jarmain 2004). Lower soil moisture may also result from higher infiltration capacity of the coarse sand fraction (Gordon *et al.* 1992) found beneath *A. mearnsii.*

The sites with *A.* mearnsii had been cleared between seven and 13 years ago and the species richness of zones, and zonal location of species, approximated that at the reference sites (Chapter 3), although some species were displaced, some were missing, and there was an over-abundance of graminoids, forbs and geophytes. Graminoids may be over-represented at invaded and cleared sites because of the elevated nutrient levels associated with the nitrogen-fixing capabilities of *A. mearnsii* (Bobbink *et al.* 1998; Yelenik *et al.* 2004) and the greater susceptibility of these riparian areas to fire (Holmes *et al.* 2005). A proliferation of graminoids has been shown to supress recruitment of invasives during restoration initiatives (Pretorius *et al.* 2008) but may also suppress recruitment of other indigenous species (Blanchard and Holmes 2008; Reinecke *et al.* 2008). Two obligate riparian trees *Salix mucronata* and *Freylinia lanceolata*, had established in the marginal and lower dynamic zones, but one characteristic restio, *Elegia capensis*, and shrub, *Erica caffra,*

had not re-established even after 13 years. This is curious since both are wind dispersed and *E. capensis* is tolerant of fire (Dorrat-Haaksma and Linder 2000) although *E. caffra* is not (Jackson 1977). Their absence may also be related to the nutrient enrichment of soils by *A. mearnsii* (Jacobs *et al.* 2013), since *E. caffra* at least does not to grow well in soils with a high nutrient content (Brown and Duncan 2006). The trees *B. stellatifolium* and *M. angustifolia* and the shrub *Diospyros glabra,* persisted during invasion and were present in the lower and upper zones at the recovering sites. However, there was also an over-abundance of the herbaceous perennial *Pteridium aquilinum,* known to colonise newly disturbed areas (Whitehead and Digby 1997). The dominance of *Pteridium aquilinum* resulted in the species richness in the lower and upper zones being lower than at the reference sites, whereas other zones were comparable. The slow recovery of the small tree guild (Holmes *et al.* 2005) is probably because these trees are re-sprouters (Galatowitsch and Richardson 2005; Holmes et al. 2005) and do not form persistent seed banks (Vosse *et al.* 2008).

The presence of invasives prior to clearing, and for some years after, disrupts the integrity of lateral vegetation zones. From a management perspective, the fact that the lower dynamic zone is the point of entry to the riparian area for alien invasives is important. Since recruitment of *Acacia* spp., and presumably other invasives, takes place first and mostly in the lower dynamic zone, focussing clearing efforts in this zone at sites with low incidence or abundance of invasives may help curb the spread of the invasive. At the same time, keeping the lower dynamic free of invasives will maximise opportunities for recruitment of small trees, the guild most impacted by the presence of the invasives. The prioritising of lightly infested areas has already been made (Marais and Wannenburgh 2008) but these results suggest that efforts in these areas could be better rewarded if they concentrate on the lower dynamic, which can be located using simple rules (Chapter 3).

7 Conclusion

The seven questions posed in the introduction to this thesis (Figure 1.1) were addressed by testing 11 hypotheses. Of these, six were supported, three were rejected and two were valid for some species and not for others.

Riparian species were indeed arranged into four distinct lateral zones parallel to river flow: two in the wet bank and two in the dry bank (Chapter 3), regardless of differences in climate or seasonal flow patterns (Chapter 4). Wet bank zones were controlled by the pattern and volume of flows in the adjacent river, but species in all zones showed some mechanical and physiological adaptations to their position on the river banks (Chapter 5). Invasives do not establish equally well in the four zones (Chapter 6).

The four lateral zones were usefully grouped into two bank types (Figure 4.12; after Boucher 2002 and Kleynhans *et al.* 2007):

- The wet bank:
    - the **marginal zone**: largely comprised of obligate riparian graminoids, trees and shrubs;
    - the l**ower dynamic zone:** a transitional area comprised of a mixture of recruitment stages of marginal and lower zone species;
- The dry bank:
    - the **lower zone**, largely comprised of facultative riparian graminoids, trees and shrubs;
    - the **upper zone**, a transitional area comprised of a mixture of lower and terrestrial species.

There was no evidence to support the hypotheses that inter-annual floods controlled the distribution of plants in the dry bank, or the period over which flowering and seed set take place. Abstraction of summer base flows did not hinder growth but with no consideration of groundwater levels, rooting depth and leaf retention this result should be interpreted with caution. In each of these cases, additional interactions with factors not considered during this dissertation may have led to rejection of the hypotheses. For example, adult riparian plants access multiple sources of water (Schachtschneider 2009). However, the results showed that recruitment flow requirements differ from water requirements *per se* and it may be that summer abstractions impact on recruitment, particularly for obligate riparian species.

Two hypotheses were only partly upheld and the reasons in both cases were attributed to the river basin signatures. When reference rivers were compared at a species level, only some species were shown to be characteristic of a zone and other species were not. Some species showed no zonal preference and overlapped across zones up the hydraulic gradient on the river bank. In other cases, a species could be a discriminating species of one zone on River A and a discriminating species for a different zone on River B (Chapter 3), although this overlap in discriminating species was less apparent when more than one riparian community was compared (Chapter 4). The variation in species abundances between zones and rivers was reduced when plants were categorized into water dependency related functional types, as the same combination of the three plant types, obligate, facultative and incidental, consistently were arranged in the same way. Assigning riparian species to functional types, based on water dependency, revealed a broad pattern in the structure of riparian vegetation communities based on functional relationships that were not masked by river signatures, biogeographical boundaries or phenotypic variation within a species. It was possible to separate the wet and dry bank hydraulically (Chapter 4) and also to demonstrate functional differences with respect to seed set and physiological tolerances to drying out between wet and dry bank species that matched predictions with respect to their position in the wet or dry bank (Chapter 5). It was not possible to separate the two dry bank zones from one another in the same way and this was expected since factors other than river flow are expected to

play an increasingly important role in the life histories of upper zone occupants (Francis 2006).

Different paths of recovery, after clearing the invasive trees *Acacia mearnsii* or *Pinus* spp., could not be solely attributed to the invasive species, as time since initiation of clearing and the different land uses of the surrounding basins were also implicated. River basin signatures were present at all sites except those most heavily invaded, which were depauperate of indigenous species. Sites invaded by *Acacia mearnsii* grouped together regardless of river basin, which indicates the indigenous vegetation was replaced to such an extent so as to override the river signatures.

In South Africa, limited funding combined with the pressing need to manage the allocation of scant water resources dictates that research is focussed on measures that inform sustainable use of the nation's water resources. The two management issues addressed in this dissertation were links between the integrity of the riparian vegetation and river flow and the mechanisms exploited by alien woody invasives to gain a foothold in riparian zones. Legislation requires on-going monitoring of the condition of the nation's river systems using the VEGRAI assessment protocol (Kleynhans *et al.* 2007). Currently, there is a dearth of riparian botanists so the rules about bank shape in relation to zonation can be used to delineate the position of the marginal, lower and upper zones, as required in VEGRAI, on headwater streams without detailed botanical knowledge. Being able to delineate lateral zones, is also important in the context of alien invasion and clearing as it allows for a direct comparison to the plants that are expected to occur naturally and can guide re-vegetation strategies of different species into the correct functional zone, based on their water dependency.

The results suggest that riparian vegetation communities respond to the flow regime in a consistent manner, regardless of geographic or climatic variation and/or species composition. The demonstrated links between the lateral zones of riparian vegetation and the timing and magnitude of river flow can be used to simulate or validate wet and dry season low flow discharge, using the marginal zone; the magnitude and duration of the intra-annual floods, using the division between the marginal and the lower dynamic zone; and the size of the 1:2 year flood, using the division between the wet and dry bank. Knowing where the zones are, which can be located using the rules, and following these natural patterns of flow and plant distribution on unregulated rivers, can inform restoration strategies and inform development planning by providing boundaries of inundation duration for the two wet bank zones and the lower boundary of the facultative tree line above the 1:2 year flood line. For example, it will not make sense to plant facultative riparian species below the 1:2 year flood line where they are likely to be flushed out. Similarly, obligate riparian species will not establish as well in the dry bank as they would in the wet bank, the zone where they naturally occur. Since the lower dynamic zone is an area where seedlings and saplings occur in high abundance, clearing efforts and other restoration activities should minimise disturbance here to avoid trampling recruiting indigenous species, which will aid the rate of recovery. Since the lower dynamic is also the point of entry for invasives into the riparian area, careful clearing of recruiting invasive species from this zone will help to retard re-invasion. *Acacia mearnsii* spreads from the lower dynamic zone up the bank through the lower and eventually into the upper zone but does not appear to establish well in the marginal zone, presumably due to the inability to persist under regular inundation and frequent flooding.

Changes to the pattern and position of zone boundaries can also provide an early warning of long-term changes to a river's flow regime and the potential for knock on effects. For example, terrestrialisation, the recruitment of incidental species into the riparian area, may take place in response to the absence of large floods and result in an increase in the incidence of fire due to a change in the litter quality (Naiman *et al.* 2008). Similarly, if the annual periods of inundation are decreased through water abstraction, obligate species may

retreat towards the waning wetted channel edge and the width of the wet bank will shrink. Since riparian pioneers are known bank stabilisers (Karrenberg *et al.* 2002; Kotschy and Rogers 2008) this could result in bank instability and it may also reduce the abundance of important species, such as wet bank graminoids, that are harvested by subsistence users (Mbaiwa 2004).

With further supporting data, it may also be possible to use zonal patterns in riparian communities and the associated average conditions about inundation duration and flood recurrence, to estimate hydraulic conditions at rivers without having to undertake hydraulic modelling. This would greatly reduce the cost, and thus the coverage, of such assessments, be they for setting environmental flows or monitoring their efficacy.

Evaluating the central question that zones result from how species respond to changing abiotic factors provided a useful framework for investigating the phenomenon of lateral zones in riparian vegetation communities. Four zones were identified conclusively but these were not exclusively determined on the basis of species differences but rather were found to occur due to unique combination of similar species within each community type. The distribution of plants in these four zones was shown to relate most strongly to river bank gradient when plant distribution in the four zones was tested against a range of physical (abiotic) site characteristics. Further investigation revealed the two wet bank zones may be separated from one another and from the dry bank conclusively by the pattern and volume of flows in the adjacent river despite differences between species and the climate and seasonal flow regime of the communities investigated. This lends further support to the idea that different species respond in the same way to flow since the same functional types, based on water dependency, were shown to occur in the different biomes. However, it was not possible to separate the two dry bank zones from one another in the same way and so attempts to validate the existence of the lower and upper zone on the basis of a direct link to river flow was not possible. Similarly, since the lower dynamic comprises a mixture of species from its two neighbours, the marginal and lower zone, it was not possible to select a characteristic species for the purposes of investigating functional differences. Functional differences were described between the wet and the dry bank species, and the two dry bank species showed variation in their response when compared with one another, which lends further support to the idea that abiotic conditions change along a lateral gradient and species are variably adapted to cope with the prevailing abiotic conditions that characterise the zone in which they occur. However, it was abundantly clear that the links to river flow were strongest at the river edge and weakened considerably into the dry bank. The transition from the wet to the dry bank may be located at an elevation and distance of 1.5 m from the wetted channel edge, or at the position of the 1:2 year flood, so further investigation of the mechanism that structures zones should be focussed in this area. The next logical step would be to investigate recruitment and the factors that control success and persistence with the framework of zones presented. This dissertation focussed on the structure of zones and provided links to abiotic characteristics that are likely to influence recruitment success but further investigation could include other water sources and additional measures of functional differences between riparian species.

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8 Appendices

8.1 Appendix Figures

The patterns of groundcovers versus trees alone differed at four sites on the Rondegat River: R1 – R4 (Chapter 3, Figure 8.1-Figure 8.4, site codes as per Table 3.1). In most cases this was due to the absence of trees from some sample plots, these outliers would thus not contribute toward the pattern. Patterns of trees showed that in some cases, sample plots situated some distance apart contained similar species. For example, a sample plot at the wetted channel edge grouped closely with a sample plot 5-m up the bank. Ground covers on the other hand were generally abundant and at each river a clear pattern of separation was evident with few outliers. Sample plots in close proximity to one another grouped strongly and in a chronological order in line with their position to the dry-season wetted channel edge.

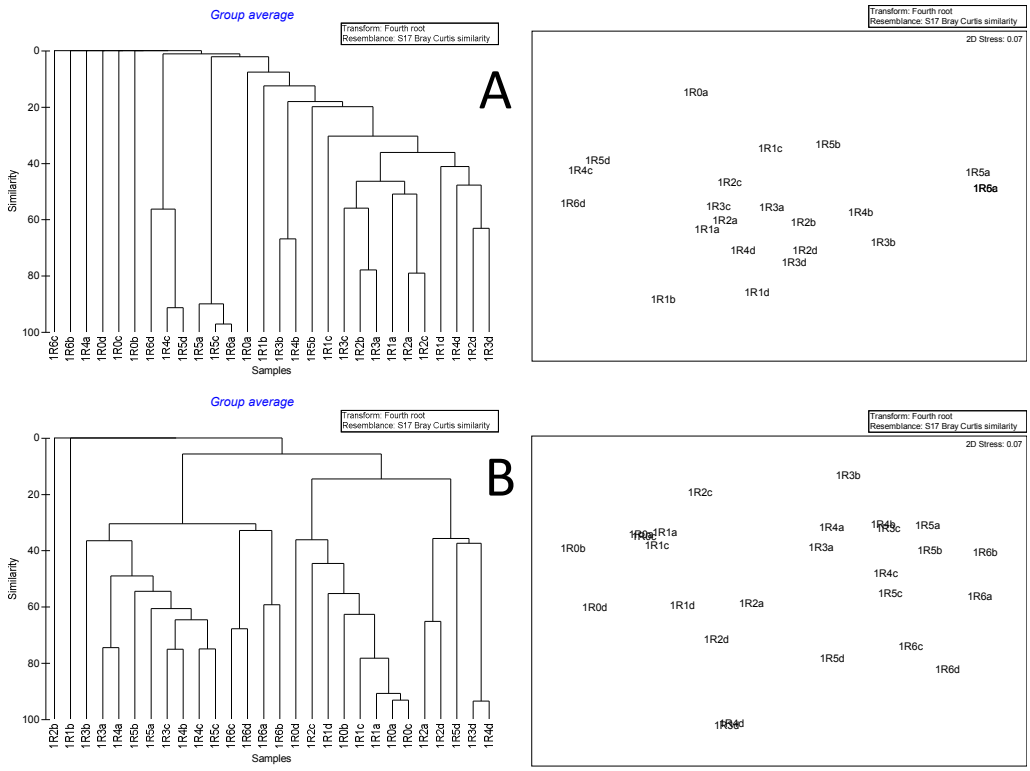

Figure 8.1 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots at R1. A = canopy, B = groundcover. Sample plot codes (e.g. 2B = metre 2 transect B), measured from the wetted channel edge.**

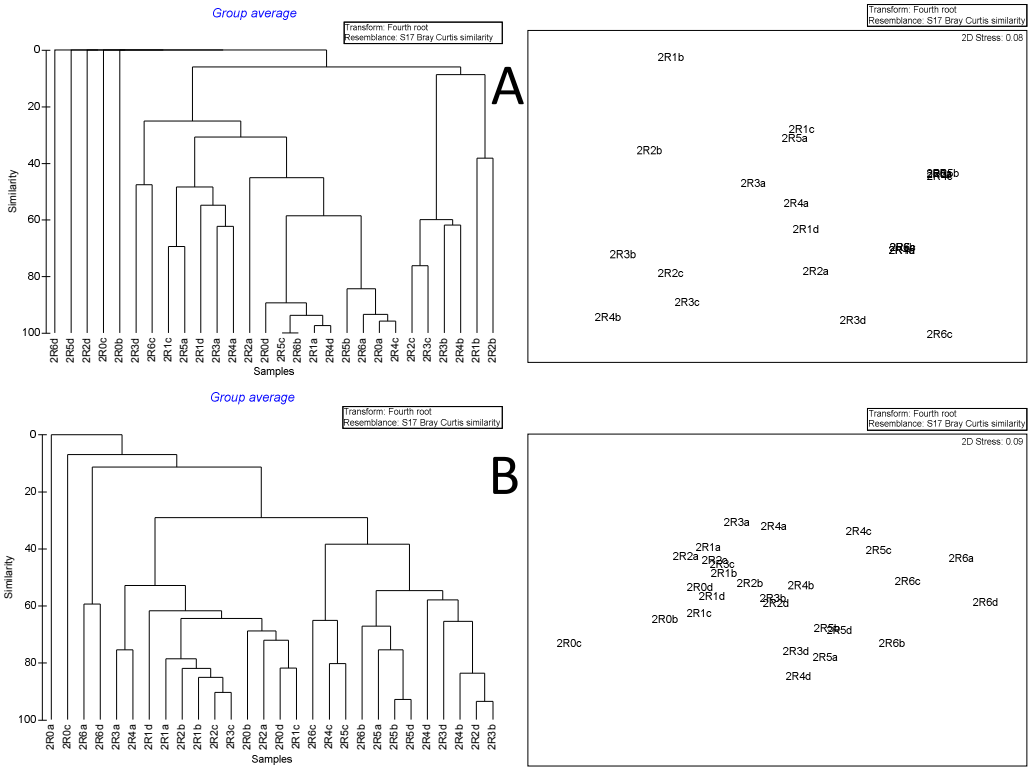

Figure 8.2 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots at R2. A = canopy, B = groundcover. Sample plot codes (e.g. 2B = metre 2 transect B), measured from the wetted channel edge.**

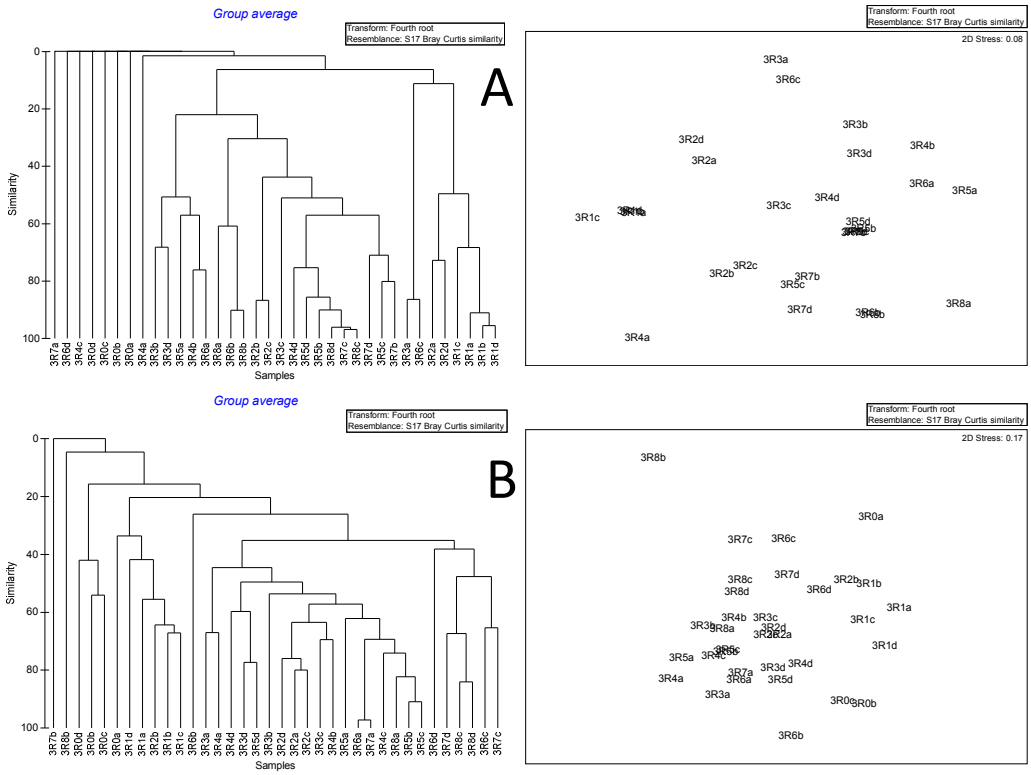

Figure 8.3 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots at R3. A = canopy, B = groundcover. Sample plot codes (e.g. 2B = metre 2 transect B), measured from the wetted channel edge.**

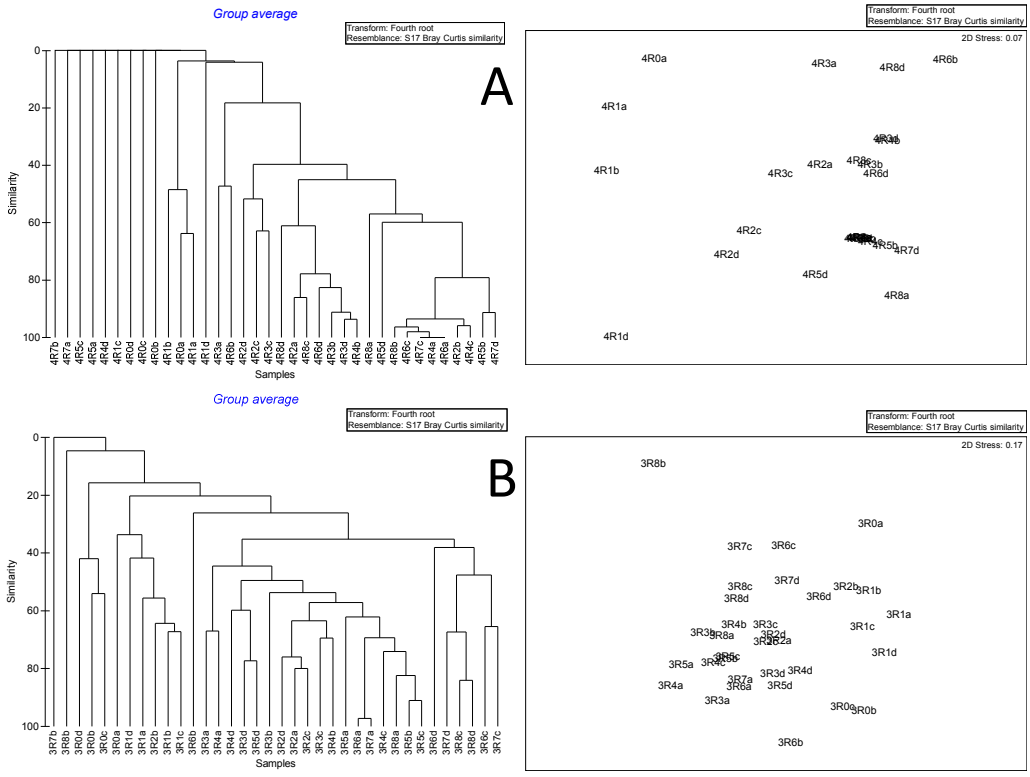

Figure 8.4 **CLUSTER analysis and MDS ordination of Bray Curtis similarity between sample plots at R4. A = canopy, B = groundcover. Sample plot codes (e.g. 2B = metre 2 transect B), measured from the wetted channel edge.**

The upper boundary between intra- and inter-annual floods, the Class 4 (green) and 1:2 year flood respectively (orange dashed), are adjacent to one another (Figure 8.5- Figure 8.13, site codes as per Table 4.1). Ten of the 18 sites demonstrated the expected relationship: that the marginal and lower dynamic were inundated by intra-annual floods and the lower and upper zone were inundated by inter-annual floods (see Chapter 4).

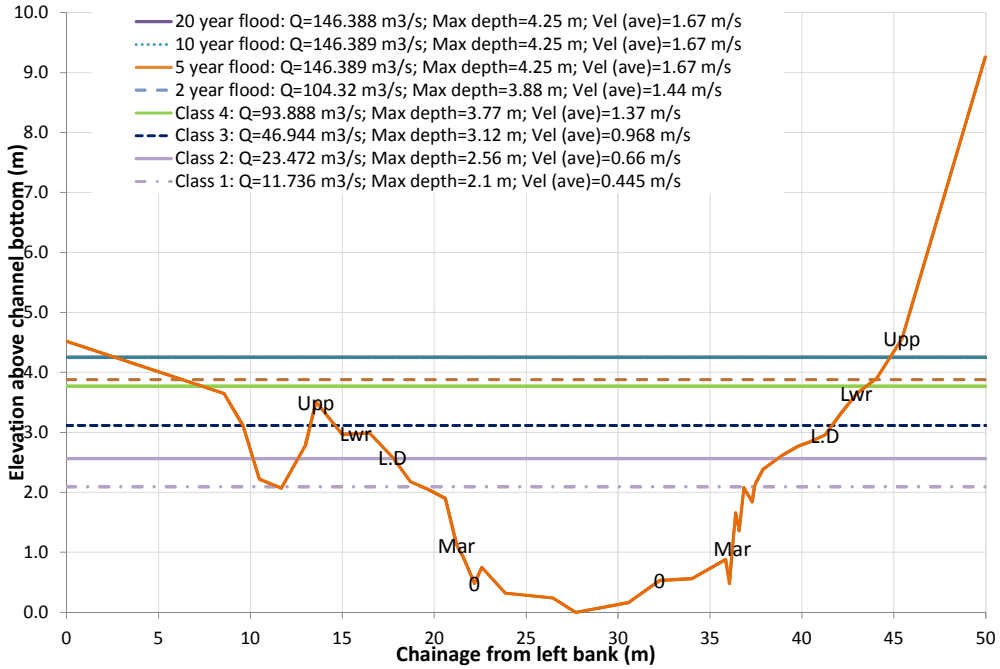

Figure 8.5 **Hydraulic cross-sections with intra- and inter annual floods that inundate each lateral zone at Mol1. 0 = lowest surveyed water level. Mar = marginal, L.D. = lower dynamic, Low = lower, Upp = upper zone.**

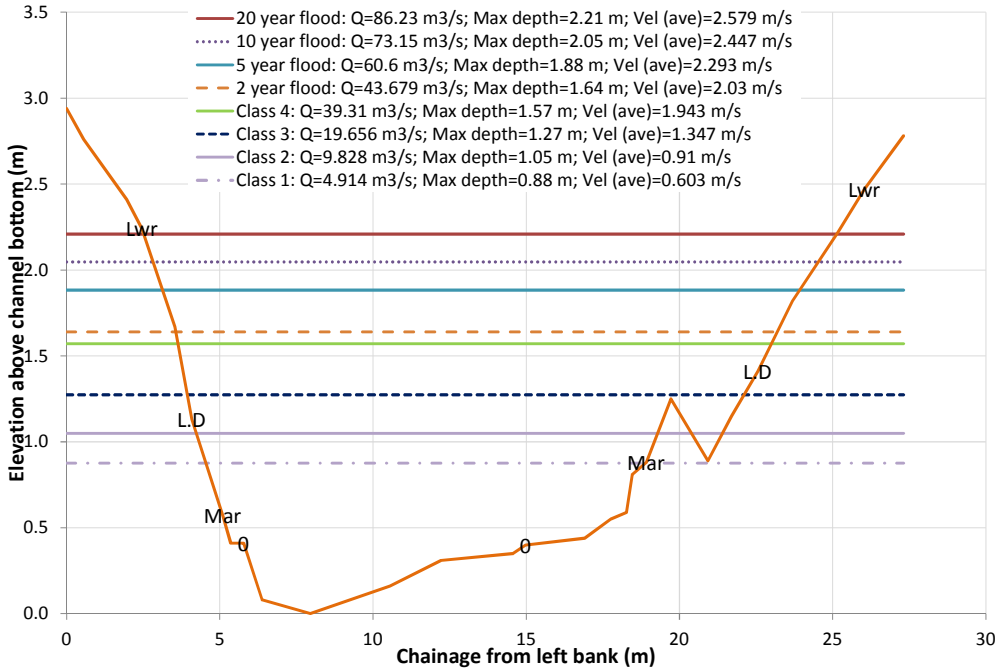

Figure 8.6 **Hydraulic cross-sections and intra- and inter annual floods that inundate each lateral zone at Ela1. 0 = lowest surveyed water level. Mar = marginal, L.D. = lower dynamic, Low = lower, Upp = upper zone.**

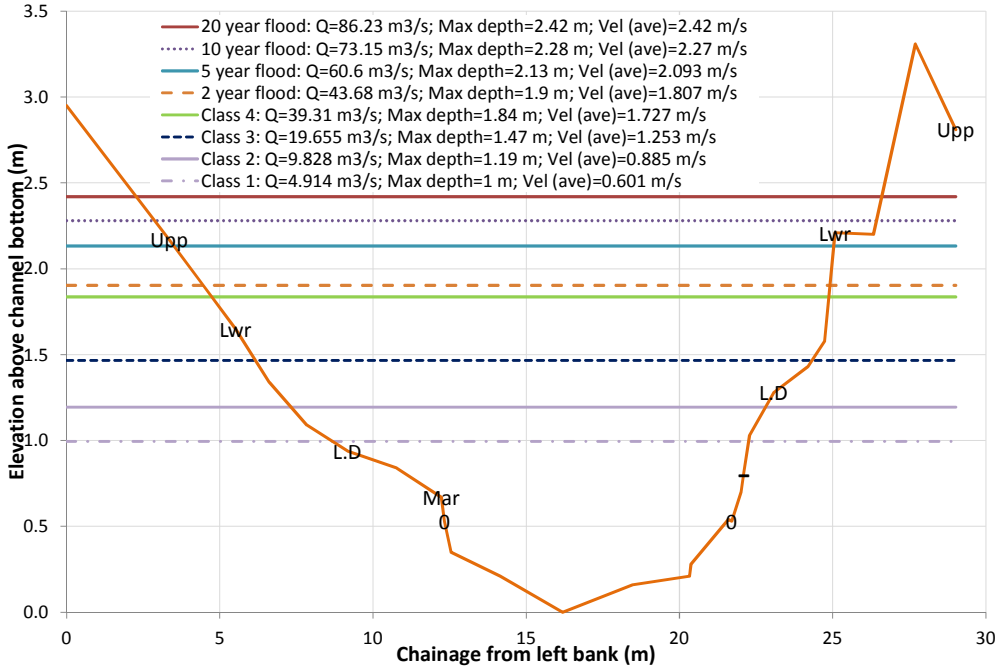

Figure 8.7 **Hydraulic cross-sections and intra- and inter annual floods that inundate each lateral zone at Ela2. 0 = lowest surveyed water level. Mar = marginal, L.D. = lower dynamic, Low = lower, Upp = upper zone.**

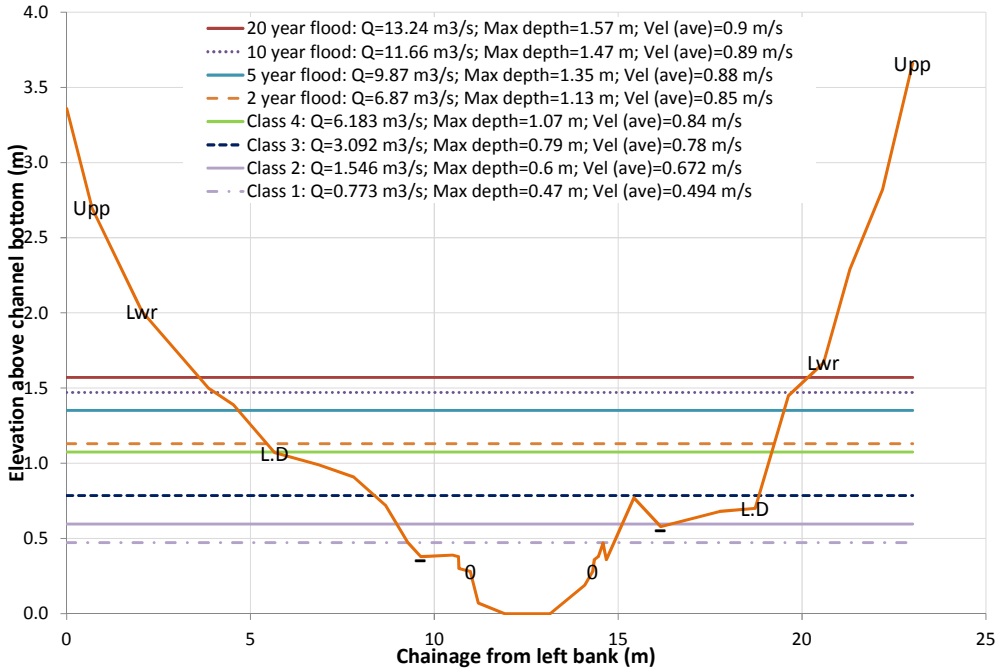

Figure 8.8 **Hydraulic cross-sections and intra- and inter annual floods that inundate each lateral zone at Kar1. 0 = lowest surveyed water level. Mar = marginal, L.D. = lower dynamic, Low = lower, Upp = upper zone.**

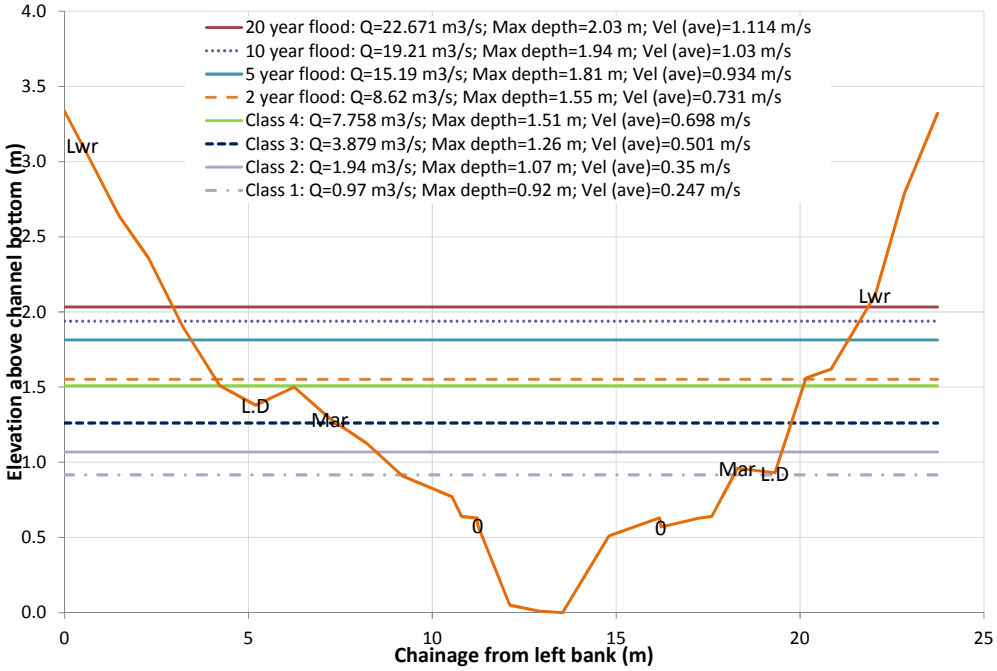

Figure 8.9 **Hydraulic cross-sections and intra- and inter annual floods that inundate each lateral zone at Kaa1. 0 = lowest surveyed water level. Mar = marginal, L.D. = lower dynamic, Low = lower, Upp = upper zone.**

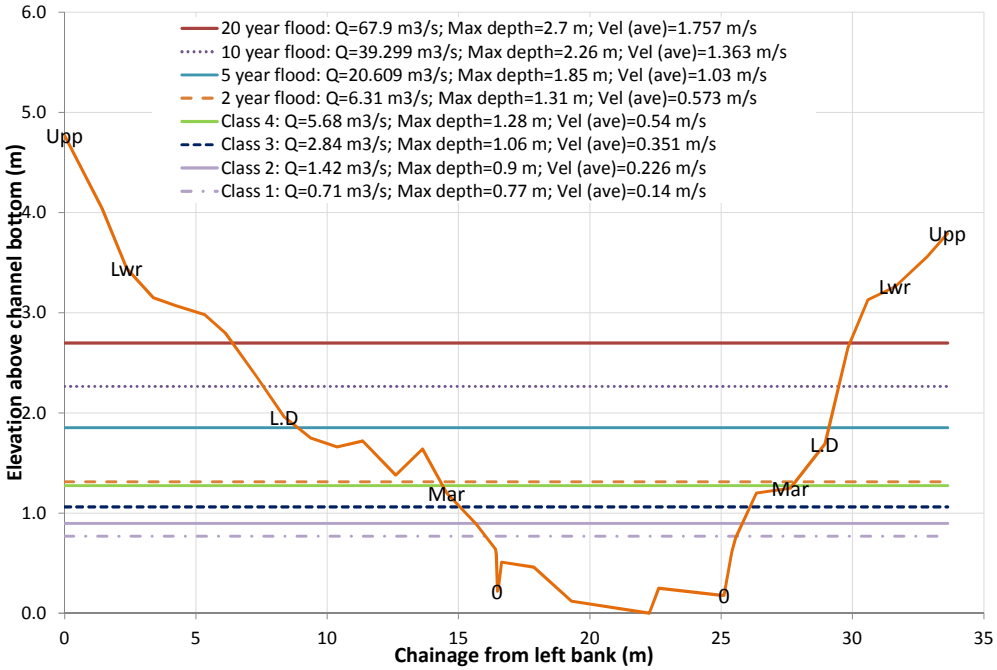

Figure 8.10 **Hydraulic cross-sections and intra- and inter annual floods that inundate each lateral zone at Die1. 0 = lowest surveyed water level. Mar = marginal, L.D. = lower dynamic, Low = lower, Upp = upper zone.**

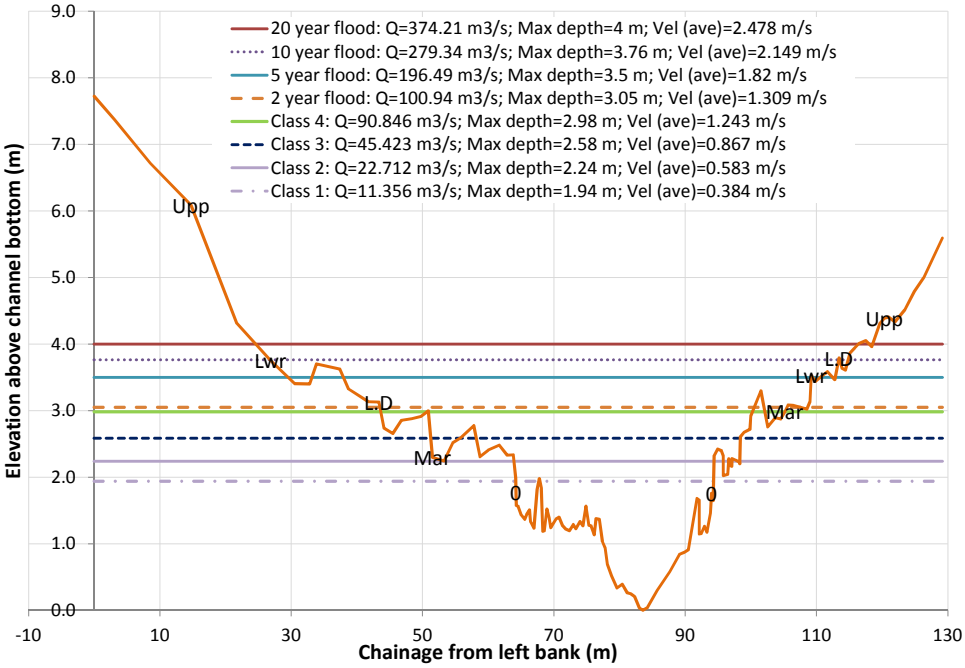

Figure 8.11 **Hydraulic cross-sections and intra- and inter annual floods that inundate each lateral zone at Cro1. 0 = lowest surveyed water level. Mar = marginal, L.D. = lower dynamic, Low = lower, Upp = upper zone.**

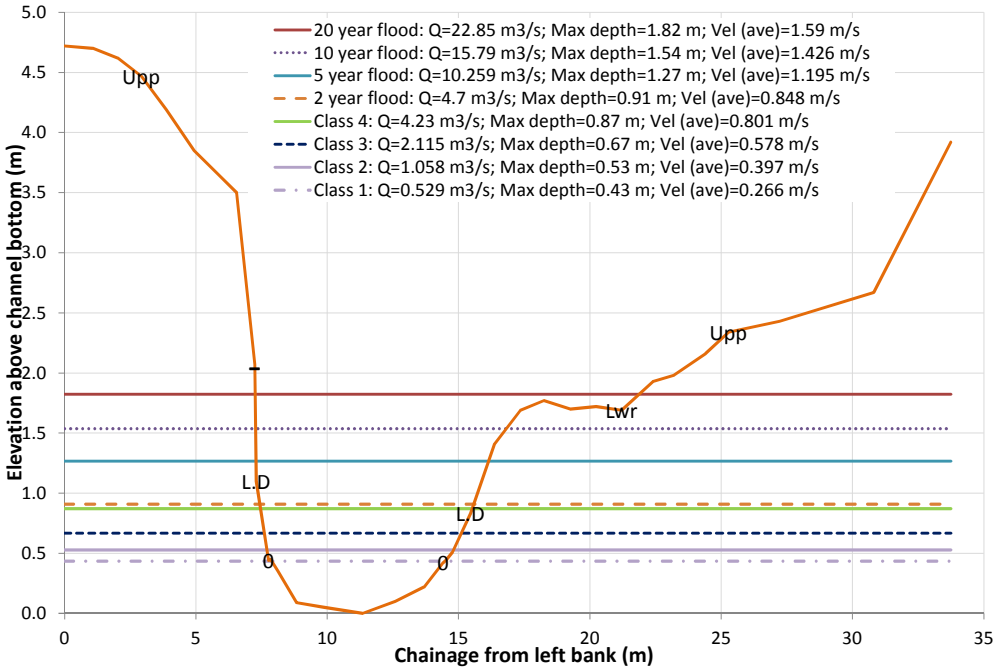

Figure 8.12 **Hydraulic cross-sections and intra- and inter annual floods that inundate each lateral zone at Mac1. 0 = lowest surveyed water level. Mar = marginal, L.D. = lower dynamic, Low = lower, Upp = upper zone.**

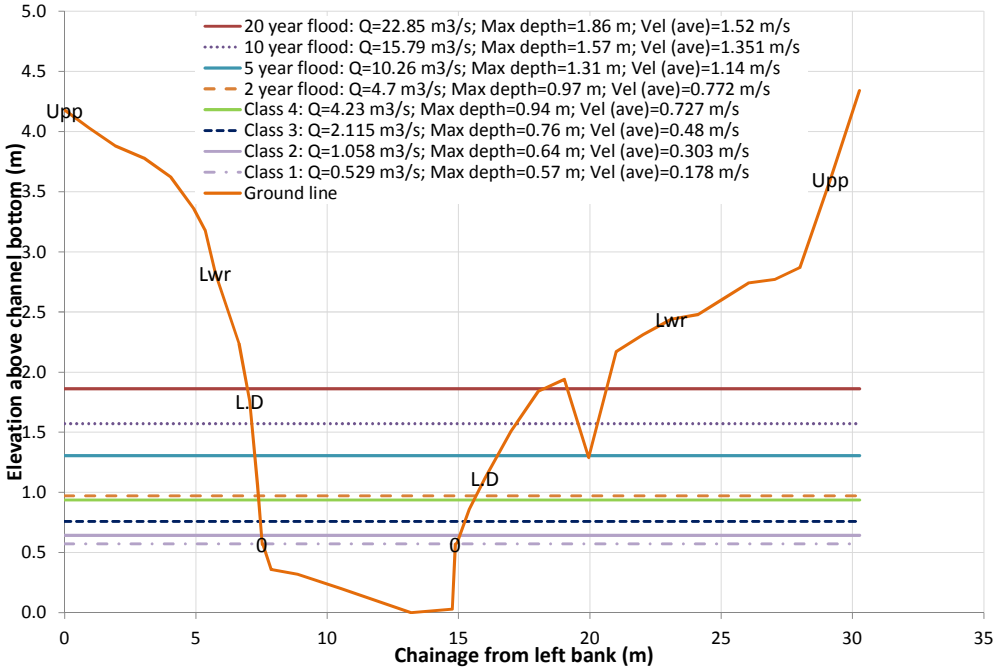

Figure 8.13 **Hydraulic cross-sections and intra- and inter annual floods that inundate each lateral zone at Mac2. 0 = lowest surveyed water level. Mar = marginal, L.D. = lower dynamic, Low = lower, Upp = upper zone.**

8.2 Appendix Tables

Table 8.1 Presence/Absence of species of Fynbos Riparian Vegetation at reference sites (Chapter 3). S = seedling, J = sapling, T = tree. Site codes as per Table 3.1.

SPECIES	R1	R2	R3	R4	H1	H2	H3	H4	W1	W2	E1	E2	E3	E4	J1	J2
Acacia mearnsii S									*							
Acacia mearnsii J									*	*						
Acacia mearnsii T										*						
Agathosma crenulata J													*			
Agathosma crenulata T			*											*		
Anthospermum spathulatum	*				*	*						*				
Arctotis revoluta						*										
Aristea capitata	*										*		*	*	*	*
Aristida junciformis										*						
Arum bract restio									*							
Askidiosperma chartaceum									*	*		*				
Asparagus africanus													*			
Asparagus rubicundus					*											*
Asparagus scandens																*
Asteraceae sp.18												*				
Asteraceae sp.19												*				
Asteraceae sp.20	*	*														
Berzelia lanuginosa									*	*						*
Blechnum attenuatum																
Blechnum australe			*	*							*					*
Blechnum capense		*		*								*	*	*	*	
Brabejum stellatifolium S	*	*	*		*		*		*		*	*	*	*		*
Brabejum stellatifolium J	*	*	*	*		*		*	*	*	*	*	*	*	*	*
Brabejum stellatifolium T	*	*	*	*		*		*	*	*	*	*	*	*	*	*
Brachylaena neriifolia S	*	*		*		*		*	*	*	*	*				
Brachylaena neriifolia J	*	*	*	*	*		*	*	*	*	*	*	*	*	*	
Brachylaena neriifolia T	*	*	*	*			*	*	*	*	*	*	*	*	*	
Calopsis paniculata	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Cannamois virgata												*		*		
Carpha glomerata					*	*										
Cassytha ciliolata									*							*
Centella sp.1										*						
Chasmanthe aethiopica																
Chelianthes contracta						*						*				
Cliffortia complanata															*	
Cliffortia cuneata															*	*
Cliffortia dregeana										*						
Cliffortia pterocarpa												*				
Cliffortia ruscifolia	*	*			*	*		*			*	*		*		
Cliffortia sp.1													*			
Clutia ericoides	*	*														
Clutia sp.1														*		
Clutia sp.2			*													

SPECIES	R1	R2	R3	R4	H1	H2	H3	H4	W1	W2	E1	E2	E3	E4	J1	J2
Crassula rupestris					*	*		*								
Cullumia ciliaris												*	*			
Cunonia capensis S											*	*				
Cunonia capensis J												*		*		*
Cunonia capensis T																*
Cyclopia sp.1											*	*	*	*	*	*
Cyperaceae sp.1													*			
Cyperaceae sp.3																*
Cyperaceae sp.5															*	*
Cyperaceae sp.6																*
Cyperaceae sp.8																*
Cyperaceae sp.9															*	
Cyperus denudatus			*		*	*	*	*								
Diospyros glabra	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*
Dodonaea viscosa S					*											
Dodonaea viscosa J	*				*	*	*									
Drosera sp.1	*		*	*			*	*			*					
Ehrharta ramosa subsp. aphylla	*								*			*				
Ehrharta rehmannii					*	*	*	*								
Ehrharta sp.4																*
Ehrharta ramosa subsp. ramosa		*	*							*	*		*			
Ehrharta sp.2									*		*	*			*	
Elegia asperiflora										*			*	*		
Elegia capensis	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Elytropappus intricata	*	*			*		*	*								
Epischoenus gracilis										*	*	*	*			
Eragrostis sarmentosa					*	*	*									
Erica bergiana												*				
Erica caffra	*	*	*	*					*	*	*	*	*	*	*	*
Erica canescens												*				
Erica curvirostris										*						
Erica hispidula									*	*					*	
Erica pinea														*		
Erica sphaeroidea															*	*
Erica tenuis										*						
Euryops abrotanifolius	*					*										
Ficinia acuminata	*	*														
Ficinia capitella																*
Ficinia indica			*		*	*		*				*				
Ficinia sp.2									*	*	*					
Ficinia trichoides																*
Freylinia lanceolata J					*	*	*	*								*
Freylinia lanceolata T					*	*	*	*								*
Hackea sericia J												*				
Hackea sericia T												*				

SPECIES	R1	R2	R3	R4	H1	H2	H3	H4	W1	W2	E1	E2	E3	E4	J1	J2
Halleria elliptica			*												*	
Halleria lucida J																*
Halleria lucida T													*			
Hartogiella schinoides J	*		*						*	*	*	*		*		*
Hartogiella schinoides T	*		*							*		*		*		*
Heeria argentea J		*							*						*	
Heeria argentea T										*						
Helichrysum odoratissimum			*										*			
Helichrysum sp.2																*
Hymenolepis sp.1										*						
Hyparrhenia hirta										*						
Ilex mitis S														*		
Ilex mitis J									*		*	*	*	*		*
Ilex mitis T											*	*	*	*		*
Indigofera sp.1									*							
Ischyrolepis fraterna									*	*			*	*		
Ischyrolepis gaudichaudianus	*					*		*								
Ischyrolepis gossypina								*								
Ischyrolepis sieberi	*				*		*				*	*			*	
Ischyrolepis subverticillata											*				*	*
Ischyrolepis tenuissima										*						
Isolepis digitata			*				*	*	*	*						
Isolepis prolifera	*	*	*	*	*	*	*	*			*					
Juncus effusus			*										*			
Juncus lomatophyllus			*	*												
Kiggelaria africana S						*										
Kiggelaria africana J			*			*										
Kiggelaria africana T																*
Laurembergia repens			*													
Leucadendron salicifolium												*	*			
Mariscus thunbergii			*	*	*	*	*	*				*				
Maytenus acuminata J														*		
Maytenus acuminata T														*		
Maytenus oleoides S			*			*	*		*							*
Maytenus oleoides J			*						*							
Merxmuellera cincta										*						
Metalasia densa												*				
Metalasia dregeana	*															
Metalasia muraltifolia										*						
Metrosideros angustifolia S	*	*	*	*	*	*	*	*	*		*	*	*			*
Metrosideros angustifolia J	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Metrosideros angustifolia T	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Mohria caffrorum															*	
Morella serrata S	*	*	*	*	*	*	*	*	*		*		*	*		
Morella serrata J	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*

SPECIES	R1	R2	R3	R4	H1	H2	H3	H4	W1	W2	E1	E2	E3	E4	J1	J2
Morella serrata T	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*
Myrsine africana	*															
Neesenbeckia punctoria																*
Nivenia corymbosa									*	*						
Oftia africana		*														
Olea sp.1 T						*										
Oscularia ornata					*	*										
Osteospermum ciliatum													*	*		
Otholobium sp.1															*	
Othonna quinquidentata										*			*	*		
Oxalis pardalis															*	
Oxalis sp.1															*	
Oxalis sp.2															*	
Panicum schinzii					*	*	*									
Paspalum urvillei			*													
Pelargonium cucullatum															*	
Pelargonium scabrum	*	*			*	*		*								
Pelargonium tabulare			*													
Pellaea pteroides															*	*
Pennisetum macrourum				*	*	*			*				*	*		
Pentachistis chandelier	*															
Pentameris distichophylla									*	*	*	*	*	*		
Pentameris thuarii										*				*	*	
Pentaschistis curvifolia										*						
Pentaschistis densifolia									*							
Pentaschistis pallida											*					
Pentaschistis sp.4	*															
Peucedanum galbanum J		*														
Phylica imberbis										*		*				
Platycaulos subcompressus									*							
Platylophus trifoliatus J											*	*	*	*		
Platylophus trifoliatus T											*	*	*	*		
Poaceae sp.4															*	*
Poaceae sp.5																*
Poaceae sp.6															*	
Podalyria sp.1											*		*	*		
Podalyria sp.3															*	
Podocarpus elongatus T										*						
Prionium serratum				*	*	*			*	*	*	*			*	*
Protea laurifolia S											*				*	
Protea laurifolia T														*		
Protea sp.1 S	*															
Protea sp.1 J	*															
Pseudobaeckia africana									*	*	*	*				
Psoralea sp.2					*	*										

SPECIES	R1	R2	R3	R4	H1	H2	H3	H4	W1	W2	E1	E2	E3	E4	J1	J2
Pteridium aquilinum	*	*	*	*					*		*	*	*		*	*
Pycreus polystachyos																*
Restio multiflorus													*			
Restio perplexus									*	*	*					
Restionaceae sp.7									*							
Restionaceae sp.8									*	*						
Restionaceae sp.9	*		*													
Searsia angustifolia			*		*	*	*	*								
Searsia crenata																*
Searsia lucida forma elliptica			*	*	*	*	*	*								
Searsia tomentosa															*	*
Rubiaceae sp.1													*	*		
Salix mucronata S					*	*							*	*		
Salix mucronata J					*								*			
Salix mucronata T													*			
Salvia sp.1						*										
Schizaea tenella	*	*									*				*	*
Species 2																*
Species 13 J														*		
Species 14															*	*
Species 15									*							
Species 16													*	*		
Species 17					*			*								
Species 18		*														
Species 19												*				
Stoebe cinerea															*	
Stoebe plumosa	*				*		*	*		*		*		*		
Stoebe spiralis													*	*		
Struthiola myrsinites																*
Taraxacum officinale															*	
Tetraria flexuosa													*			
Thamnochortus lucens														*		
Thamnochortus sp.1									*	*						
Thesium sp.1	*															
Todea barbara	*	*	*	*					*	*	*	*	*	*	*	
Tribolium uniolae										*						
Ursinia abrotanifolia										*		*	*			
Ursinia pinnata										*						
Wahlenbergia rubiodes	*															
Phylica oleaefolia S	*															
Phylica oleaefolia J	*					*										
Phylica oleaefolia T					*	*		*								
Wildenowia glomerata									*	*						
Wildenowia incurvata	*	*						*								
Wimmerella arabidea			*	*		*										

SPECIES	R1	R2	R3	R4	H1	H2	H3	H4	W1	W2	E1	E2	E3	E4	J1	J2
Zyrphelis montana										*						

Table 8.2 Habitat characteristics for species of Fynbos Riparian Vegetation at reference rivers (Chapter 3).

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESIGNATION	COMMON NAME
Anthospermum spathulatum	Rubiaceae	Shrub	Clay slopes, DRY	Incidental	
Arctotis revoluta	Asteraceae	Shrub	Rocky slopes, DRY	Incidental	Krulblaargousblom
Aristea capitata	Iridaceae	Forb	Mountain slopes, DRY	Incidental	Blousuurkanol
Aristida junciformis	Poaceae	Grass	Mountain slopes, DRY	Incidental	Wire grass
Askidiosperma chartaceum	Restionaceae	Restio	Marshy mountain slopes, WET	Obligate	
Asparagus africanus	Asparagaceae	Shrub	Moist places, WET	Obligate	Katdoring
Asparagus rubicundus	Asparagaceae	Shrub	Sandy and granite slopes, DRY	Incidental	Katdoring
Asparagus scandens	Asparagaceae	Shrub	Forest	Facultative	Katdoring
Berzelia lanuginosa	Bruniaceae	Shrub	Riverine, WET	Obligate	Berzelia
Blechnum attenuatum	Blechnaceae	Forb	Forest	Facultative	Deer fern
Blechnum australe	Blechnaceae	Forb	Forest	Facultative	Southern deer fern
Blechnum capense	Blechnaceae	Forb	Riverine, WET	Obligate	Cape deer fern
Brabejum stellatifolium	Proteaceae	Tree	Riverine, WET	Obligate	Wild *B. stellatifolium*
Brachylaena neriifolia	Asteraceae	Small tree	Riverine, WET	Obligate	Bitterblaar
Calopsis paniculata	Restionaceae	Restio	Riverine, WET	Obligate	
Cannamois virgata	Restionaceae	Restio	Riverine, WET	Obligate	
Cassytha ciliolata	Lauraceae	Forb	Various trees and shrubs, DRY	Incidental	False dodder
Chasmanthe aethiopica	Iridaceae	Geophyte	Coastal, bush, forest	Facultative	Cobra lily
Chelianthes contracta	Pteridaceae	Forb	Shady rocks, DRY	Incidental	Lip Fern
Cliffortia complanata	Rosaceae	Small shrub	Moist upper rocky slopes, WET	Obligate	Climber's Friend
Cliffortia cuneata	Rosaceae	Shrub	Lower sandstone slopes, DRY	Incidental	Climber's Friend
Cliffortia dregeana	Rosaceae	Shrub	Sandstone slopes, DRY	Incidental	Climber's Friend
Cliffortia pterocarpa	Rosaceae	Shrub	Lower mountain slopes, DRY	Incidental	Climber's Friend
Cliffortia ruscifolia	Rosaceae	Shrub	Rocky sandstone soils, DRY	Incidental	Steekbos
Cyperus denudatus	Cyperaceae	Sedge	Riverine, WET	Obligate	
Diospyros glabra	Ebenaceae	Shrub	Sandy flats and slopes, DRY	Incidental	Bloubesiebos
Diospyros whyteana	Ebenaceae	Small tree	Slopes, DRY	Incidental	Bladder-nut

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESIGNATION	COMMON NAME
Dodonaea viscosa	Sapindaceae	Tree	Riverine thicket and rocky outcrops, WET	Obligate	Sand olive
Ehrharta ramosa subsp. aphylla	Poaceae	Grass	Mountain slopes, DRY	Incidental	
Ehrharta ramosa subsp. ramosa	Poaceae	Grass	Mountain slopes, DRY	Incidental	
Ehrharta rehmannii	Poaceae	Grass	Mountain slopes, forest margins, DRY	Incidental	
Elegia asperiflora	Restionaceae	Restio	Seeps on sandstone slopes, WET	Obligate	
Elegia capensis	Restionaceae	Restio	Riverine, WET	Obligate	
Elytropappus intricata	Asteraceae	Shrub	Sandstone slopes, DRY		Renosterbos
Epischoenus gracilis	Cyperaceae	Sedge	Mountain slopes, DRY	Incidental	
Eragrostis sarmentosa	Poaceae	Grass	Winter-wet sand, WET	Obligate	Love grass
Erica bergiana	Ericaceae	Small shrub	Seeps and moist slopes, WET	Obligate	Heather
Erica caffra	Ericaceae	Shrub	Riverine, WET	Obligate	Water heath
Erica canescens	Ericaceae	Small shrub	Coastal flats and lower slopes, DRY	Incidental	Heather
Erica curvirostris	Ericaceae	Small shrub	Dry stony areas, DRY	Incidental	Heuningheide
Erica hispidula	Ericaceae	Small shrub	Widespread, DRY	Incidental	Heather
Erica pinea	Ericaceae	Small shrub	Rocky slopes and plateaus, DRY	Incidental	Heather
Erica sphaeroidea	Ericaceae	?	?		Heather
Erica tenuis	Ericaceae	Small shrub	Rocky wet ledges to open slopes, DRY	Incidental	Heather
Euryops abrotanifolius	Asteraceae	Forb	Weed		Geelmagriet
Ficinia acuminata	Cyperaceae	Sedge	Riverine, WET	Obligate	
Ficinia capitella	Cyperaceae	Sedge	Flats and slopes, DRY	Incidental	
Ficinia indica	Cyperaceae	Sedge	Flats and lower slopes, DRY	Incidental	
Ficinia trichoides	Cyperaceae	Sedge	Rocky lower to middle slopes, DRY	Incidental	
Freylinia lanceolata	Scrophulariaceae	Small tree	Riverine, WET	Obligate	Heuningklokkiebos
Hackea sericea	Proteaceae	Small tree	Sandstone slopes, DRY	Incidental	Silky hakea
Halleria elliptica	Scrophulariaceae	Shrub	Riverine slopes, WET	Obligate	Fuschia
Halleria lucida	Scrophulariaceae	Small tree	Coastal bush, forest	Facultative	Tree fuschia
Hartogiella schinoides	Celastraceae	Small tree	Fynbos, forest, woodland, DRY	Incidental	Saffron
Heeria argentea	Anacardiaceae	Tree	Rocky forest and bush, DRY	Incidental	Kliphout

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESIGNATION	COMMON NAME
Helichrysum odoratissimum	Asteraceae	Small shrub	Sandy slopes in damp places, DRY	Incidental	Strooiblom
Hyparrhenia hirta	Poaceae	Grass	Disturbed areas and grassland, DRY	Incidental	Thatch grass
Ilex mitis	Aquifoliaceae	Tree	Riverine Forest, WET	Obligate	African holly
Ischyrolepis fraterna	Restionaceae	Restio	?		
Ischyrolepis gaudichaudianus	Restionaceae	Restio	Dry rocky slopes, DRY	Incidental	
Ischyrolepis gossypina	Restionaceae	Restio	Light seeps and moist slopes, WET	Obligate	
Ischyrolepis sieberi	Restionaceae	Restio	Rocky slopes and flats, DRY	Incidental	
Ischyrolepis tenuissima	Restionaceae	Restio	?		
Ischyrolepis subverticulata	Restionaceae	Restio	Riverine, WET	Obligate	
Isolepis digitata	Cyperaceae	Sedge	Riverine, WET	Obligate	
Isolepis prolifera	Cyperaceae	Sedge	Riverine, WET	Obligate	
Juncus effusus	Juncaceae	Rush	Riverine, WET	Obligate	
Juncus lomatophyllus	Juncaceae	Rush	Riverine, WET	Obligate	
Kiggelaria africana	Kiggelariaceae	Tree	Forest, DRY	Incidental	Wild Peach
Laurembergia repens	Haloragaceae	Forb	Boggy, WET	Obligate	
Leucadendron salicifolium	Proteaceae	Shrub	Riverine, WET	Obligate	Cone bush
Mariscus thunbergii	Cyperaceae	Sedge	Riverine, WET	Obligate	
Maytenus acuminata	Celastraceae	Small tree	Forest margins or rocky slopes, DRY	Incidental	Sybas
Maytenus oleoides	Celastraceae	Small tree	Rocky slopes, DRY	Incidental	Klipkershout
Merxmuellera cincta	Poaceae	Grass	Riverine, WET	Obligate	
Metalasia densa	Asteraceae	Shrub	Sandy or stony flats and slopes, DRY	Incidental	Blombos
Metalasia dregeana	Asteraceae	Shrub	Sandstone and clay slopes, DRY	Incidental	Blombos
Metalasia muraltifolia	Asteraceae	Shrub	Sandstone slopes, DRY	Incidental	Blombos
Metrosideros angustifolia	Myrsinaceae	Small tree	Riverine, WET	Obligate	Smalblad
Mohria caffrorum	Anemiaceae	Forb	Fynbos and renosterveld, DRY	Incidental	Scented fern
Morella serrata	Myricaceae	Small tree	Coastal sandy and limestone flats, DRY	Incidental	Waterolier
Myrsine africana	Myrsinaceae	Shrub	Sandy flats and slopes in scrub, DRY	Incidental	Cape *M. angustifolia*
Neesenbeckia punctoria	Cyperaceae	Sedge	Riverine, WET	Obligate	

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESIGNATION	COMMON NAME
Nivenia corymbosa	Iridaceae	Shrub	Riverine, WET	Obligate	Bush iris
Oftia africana	Scrophulariaceae	Small shrub	Rocky sandstone/granite slopes, DRY	Incidental	
Olea europea	Oleaceae	Tree	Forests and rocky slopes, DRY	Incidental	
Oscularia ornata	Aizoaceae	Small shrub	Rock crevices, DRY	Incidental	Sandsteenvygie
Osteospermum ciliatum	Asteraceae	Small shrub	Sandstone slopes, DRY	Incidental	Bietou
Othonna quinquidentata	Asteraceae	Shrub	Rocky sandstone slopes, DRY	Incidental	Bobbejaankool
Oxalis pardalis	Oxalidaceae	Geophyte	Heavier soils, DRY	Incidental	Sorrel
Panicum schinzii	Poaceae	Grass	Moist sites, WET	Obligate	Blousaadgras
Paspalum urvillei	Poaceae	Grass	Riverine, WET	Obligate	Dallis grass
Pelargonium scabrum	Geraniaceae	Shrub	Rocky sandstone slopes, DRY	Incidental	Hoenderbos
Pelargonium tabulare	Geraniaceae	Small shrub	Cool slopes, DRY	Incidental	Malva
Pellaea pteroides	Pteridaceae	Forb	Forest, fynbos	Facultative	*M. angustifolia* fern
Pennisetum macrourum	Poaceae	Grass	Marshes, WET	Obligate	Bedding grass
Pentameris distichophylla	Poaceae	Grass	Rocky sandstone slopes, DRY	Incidental	
Pentameris thuarii	Poaceae	Grass	Lower sandstone slopes, DRY	Incidental	
Pentaschistis curvifolia	Poaceae	Grass	Sandstones slopes, DRY	Incidental	
Pentaschistis densifolia	Poaceae	Grass	Sandstone ledges and rock cracks, DRY	Incidental	
Pentaschistis pallida	Poaceae	Grass	Slopes and flats, DRY	Incidental	
Peucedanum galbanum	Apiaceae	Small tree	Rocky slopes, forest, bush, DRY	Incidental	Blister bush
Phylica imberbis	Rhamnaceae	Shrub	Sandstone slopes and flats, DRY	Incidental	Hardebos
Phylica oleaefolia	Rhamnaceae	Shrub	Rocky slopes, DRY	Incidental	Blinkhardebos
Pinus pinaster	Pinaceae	Tree	EXOTIC		Cluster pine
Pinus radiata	Pinaceae	Tree	EXOTIC		
Platycaulos subcompressus	Restionaceae	Restio	?		
Platycaulus major	Restionaceae	Restio	?		
Platylophus trifoliatus	Cunoniaceae	Tree	Riverine, WET	Obligate	Witels
Prionium serratum	Prioniaceae	Shrub	Riverine, WET	Obligate	Palmiet
Protea laurifolia	Proteaceae	Tree	Sandstone slopes, DRY	Incidental	Protea

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESIGNATION	COMMON NAME
Pseudobaeckia africana	Bruniaceae	Shrub	Riverine, WET	Obligate	
Pseudoselago verbenacea	Scrophulariaceae	Forb	Riverine, WET	Obligate	Powder puff
Pteridium aquilinum	Dennstaedtiaceae	Forb	Fynbos, forest	Facultative	Bracken fern
Pycreus polystachyos	Cyperaceae	Sedge	Damp, WET	Obligate	
Restio multiflorus	Restionaceae	Restio	?		
Restio perplexus	Restionaceae	Restio	?		
Searsia angustifolia	Anacardiaceae	Small tree	Riverine, WET	Obligate	Wilgerkorentebos
Searsia crenata	Anacardiaceae	Small tree	Sandy coastal flats. DRY	Incidental	Duinekraaibessie
Searsia lucida	Anacardiaceae	Small tree	Sandy flats and slopes, DRY	Incidental	Blinktaaibos
Searsia tomentosa	Anacardiaceae	Small tree	Rocky slopes, DRY	Incidental	Korentebos
Salix mucronata	Saliaceae	Small tree	Riverine, WET	Obligate	Cape *S. mucronata*
Schizaea tenella	Schizaeaceae	Forb	Riverine, WET	Obligate	Toothbrush fern
Stoebe cinerea	Asteraceae	Shrub	Rocky slopes, DRY	Incidental	Vaal hartebeeskaroo
Stoebe plumosa	Asteraceae	Shrub	Rocky flat and slopes, DRY	Incidental	Slangbos
Stoebe spiralis	Asteraceae	Small shrub	Damp sandstone slopes, DRY	Incidental	Hartebeeskaroo
Struthiola myrsinites	Thymelaeaceae	Shrub	Sandy soils, DRY	Incidental	Featherhead
Taraxacum officinale	Asteraceae	Forb	Weed		
Tetraria flexuosa	Cyperaceae	Sedge	Flats to middle slopes, DRY	Incidental	
Thamnochortus lucens	Restionaceae	Restio	?		
Todea barbara	Osmundaceae	Forb	Riverine, WET	Obligate	
Tribolium uniolae	Poaceae	Grass	Clay and granite flats, DRY	Incidental	Koringgras
Ursinia abrotanifolia	Asteraceae	Shrub	Sandstone slopes in damp places, DRY	Incidental	Fynkruie
Ursinia pinnata	Asteraceae	Shrub	Riverine, WET	Obligate	Bergmargriet
Wahlenbergia rubiodes	Campanulaceae	Small shrub	High rocky slopes, DRY	Incidental	African blue-bell
Wildenowia glomerata	Restionaceae	Restio	?		
Wildenowia incurvata	Restionaceae	Restio	Sandy coastal flats, DRY	Incidental	
Wimmerella arabidea	Campanulaceae	Forb	Water, WET	Obligate	
Zyrphelis montana	Asteraceae	Shrub	Sandstone slope, DRY	Incidental	Pluimastertjie

Table 8.3 Presence/Absence of species of Fynbos Riparian Vegetation at invaded (Chapter 6) sites. S = seedling, J = sapling, T = tree. Site codes as per Table 6.1.

SPECIES	cM1	cM2	cM3	iM4	iW3	cW4	cR5	iR6	cA1	iA2	cA3	cS1	cS2	i$1	i$2
Acacia mearnsii S									*						
Acacia mearnsii J									*	*					
Acacia mearnsii T										*					
Agathosma crenulata J													*		
Agathosma crenulata T			*											*	
Anthospermum spathulatum	*				*	*						*			
Arctotis revoluta						*									
Aristea capitata	*										*		*	*	*
Aristida junciformis										*					
Arum bract restio									*						
Askidiosperma chartaceum									*	*		*			
Asparagus africanus													*		
Asparagus rubicundus					*										
Asparagus scandens															
Asteraceae sp.18												*			
Asteraceae sp.19												*			
Asteraceae sp.20	*	*													
Berzelia lanuginosa									*	*					
Blechnum attenuatum															
Blechnum australe			*	*							*				
Blechnum capense		*		*								*	*	*	*
Brabejum stellatifolium S	*	*	*		*		*		*		*	*	*	*	
Brabejum stellatifolium J	*	*	*	*		*		*	*	*	*	*	*	*	*
Brabejum stellatifolium T	*	*	*	*		*		*	*	*	*	*	*	*	*
Brachylaena neriifolia S	*	*		*		*		*	*	*	*	*			
Brachylaena neriifolia J	*	*	*	*	*		*	*	*	*	*	*	*	*	*
Brachylaena neriifolia T	*	*	*	*			*	*	*	*	*	*	*	*	*
Calopsis paniculata	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Cannamois virgata												*		*	
Carpha glomerata					*	*									
Cassytha ciliolata									*						
Centella sp.1										*					
Chasmanthe aethiopica															
Chelianthes contracta						*						*			
Cliffortia complanata															*
Cliffortia cuneata															*
Cliffortia dregeana										*					
Cliffortia pterocarpa												*			
Cliffortia ruscifolia	*	*			*	*		*			*	*		*	
Cliffortia sp.1													*		
Clutia ericoides	*	*													
Clutia sp.1														*	
Clutia sp.2			*												

SPECIES	cM1	cM2	cM3	iM4	iW3	cW4	cR5	iR6	cA1	iA2	cA3	cS1	cS2	i$1	l$2
Crassula rupestris					*	*		*							
Cliffortia atrata							*								
Cliffortia dregeana			*												
Cliffortia phillipsii															*
Cliffortia polygonifolia															*
Cliffortia ruscifolia					*										
Cliffortia subsetacea													*		
Clutia sp.1			*												
Convolvulaceae sp.1									*						
Conyza bonariensis												*			
Conyza canadensis									*	*	*	*	*		
Conyza sp.1										*					
Conyza sp.2						*	*								
Cryptocarya angustifolia J							*			*					
Cryptocarya angustifolia T							*			*					
Cullumia setosa															*
Cunonia capensis S													*		
Cunonia capensis J									*				*		
Cunonia capensis T													*		
Cyperaceae sp.1										*					
Cyperaceae sp.3									*						
Cyperaceae sp.4				*											
Cyperaceae sp.7												*			
Cyperaceae sp.10												*	*		
Cyperus denudatus		*			*										
Digitaria debilis									*	*		*			
Digitaria sanguinalis							*	*			*				
Diospyros glabra	*	*	*	*	*	*	*			*	*			*	*
Drosera sp.1							*								
Ehrharta ramosa											*				*
Ehrharta ramosa subsp. *aphylla*												*		*	
Ehrharta setacea												*	*	*	*
Ehrharta sp.3								*							
Ehrharta sp.5						*	*								
Ehrharta ramosa subsp. *ramosa*	*	*	*		*										
Ehrharta sp.2									*	*					
Elegia capensis					*										
Eragrostis curvula						*	*	*						*	
Erica abietina subsp. *atrorsea*												*			
Erica bergiana															
Erica caffra							*	*				*			
Erica curviflora												*			
Erica laeta												*	*		
Erica nudiflora						*									
Eucalyptus leucoxylon J															

SPECIES	cM1	cM2	cM3	iM4	iW3	cW4	cR5	iR6	cA1	iA2	cA3	cS1	cS2	i$1	I$2
Eucalyptus leucoxylon T															
Fabaceae sp.1								*							
Ficinia capillifolia										*					
Ficinia capitella							*								
Ficinia indica			*		*										
Ficinia nigrescens										*					*
Ficinia oligantha													*		
Ficinia sp.1				*											
Ficinia sp.2			*								*				
Ficinia tenuifolia												*			
Ficinia trichoides										*	*				*
Freylinia lanceolata J							*	*							*
Freylinia lanceolata T						*		*							
Fuirena hirsuta												*		*	*
Gallium sp.1											*				
Gastridium phleoides											*				
Gnaphalium sp.1						*	*								
Grammatotheca bergiana								*							
Halleria elliptica	*					*	*		*	*	*				*
Hartogiella schinoides S										*					
Hartogiella schinoides J										*					
Hartogiella schinoides T										*					
Helichrysum cymosum												*	*	*	*
Helichrysum odoratissimum									*	*					
Helichrysum patulum															*
Helichrysum sp.2											*				
Helichrysum sp.3											*				
Hippia frutescens											*				
Hippia sp.1									*						
Histiopteris incisa					*				*	*	*	*	*	*	*
Hydrocotyle verticillata														*	*
Hymenolepis sp.1					*	*									
Ilex mitis J							*			*					
Ilex mitis T										*					
Indigofera filifolia													*		
Indigofera sp.1						*									
Inula graveolens											*				
Ischyrolepis cincinnata												*	*		
Ischyrolepis macer														*	
Ischyrolepis subverticillata									*	*					*
Ischyrolepis subverticulata															*
Isolepis digitata					*										
Isolepis ludwigii													*		
Isolepis prolifera			*	*		*	*	*	*	*	*	*	*	*	*
Isolepis sp.1									*	*					

SPECIES	cM1	cM2	cM3	iM4	iW3	cW4	cR5	iR6	cA1	iA2	cA3	cS1	cS2	i$1	l$2
Juncus capensis							*	*	*	*	*	*	*	*	*
Juncus effusus			*	*		*	*	*	*	*	*	*	*		
Juncus exsertus					*				*	*	*				
Juncus lomatophyllus			*	*	*	*	*	*	*	*	*				
Kiggelaria africana S										*					
Kiggelaria africana J															
Kiggelaria africana T										*					
Lagurus ovatus													*		
Laurembergia repens					*		*					*	*		
Leucadendron salicifolium						*									*
Mariscus thunbergii					*										
Maytenus acuminata S													*		
Maytenus acuminata J													*		*
Maytenus acuminata T													*		
Maytenus oleoides S										*					
Maytenus oleoides T										*					
Merxmuellera cincta			*												
Metalasia densa											*				
Metalasia sp.1															*
Metrosideros angustifolia S		*	*	*	*		*	*	*		*				
Metrosideros angustifolia J	*	*	*	*	*	*	*	*	*	*	*				
Metrosideros angustifolia T	*	*	*	*	*	*	*	*	*	*					
Morella serrata S	*	*					*								
Morella serrata J	*	*	*			*	*	*							
Morella serrata T	*		*		*	*		*							
Muraltia sp.1															*
Myrsine africana													*		
Neesenbeckia punctoria															*
Nemesia affinis															*
Nemesia diffusa											*				
Oftia africana					*	*		*	*		*		*		*
Oncinema lineare							*								
Osmitopsis asteriscoides															*
Osteospermum ciliatum											*				*
Osteospermum hispidum											*				
Othonna parviflora												*			*
Panicum schinzii						*		*							
Paraserianthes lophantha S								*							
Paraserianthes lophantha J						*		*							
Paraserianthes lophantha T						*									
Paspalum dilatatum												*			
Paspalum urvillei			*		*	*	*	*	*	*	*		*	*	*
Passerina vulgaris												*	*		
Pelargonium capitatum												*			*
Pelargonium cucullatum											*	*	*		

SPECIES	cM1	cM2	cM3	iM4	iW3	cW4	cR5	iR6	cA1	iA2	cA3	cS1	cS2	i$1	I$2
Pelargonium cucullatum										*					
Pelargonium grossularioides															*
Pelargonium sp.1										*					
Pelargonium tabulare											*				
Pennisetum clandestinum													*	*	
Pennisetum macrourum					*	*	*	*				*			*
Pentameris distichophylla	*		*												
Pentameris thuarii			*												
Pentaschistis airoides												*		*	
Pentaschistis aurea					*										
Pentaschistis barbata														*	*
Pentaschistis pallida			*												
Pentaschistis sp.1				*		*									
Persicaria lapathifolia				*		*	*	*							
Phytolacca americana											*				
Phytolacca octandra									*	*					
Pinus pinaster B													*		
Platycaulos callistachyus						*	*								
Platycaulus compressus												*		*	*
Plecostachys polifolia						*		*	*					*	*
Pleopeltis macrocarpa									*	*					
Poaceae sp.1				*											
Poaceae sp.2						*		*							
Poaceae sp.3						*	*								
Podalyria sp.1											*				
Podalyria sp.3														*	
Podalyria sp.4										*					
Podocarpus elongatus S		*													
Podocarpus elongatus J	*			*											
Podocarpus elongatus T	*			*											
Prionium serratum	*	*	*	*	*	*	*	*							*
Pseudobaeckia africana			*		*										
Pseudognaphalium luteo-album										*					
Pseudognaphalium undulatum											*				
Pseudopentameris thuarii											*				
Pseudoselago recurvifolia					*						*				
Pseudoselago subglabra											*				
Pseudoselago verbenacea											*				
Psoralea pinnata												*	*		
Psoralea sp.1						*									
Psoralea sp.2					*						*				*
Psoralea sp.3									*						
Pteridium aquilinum		*			*	*	*			*				*	*
Pycreus polystachyos					*		*					*			
Rapanea melanophloeos S										*			*		

SPECIES	cM1	cM2	cM3	iM4	iW3	cW4	cR5	iR6	cA1	iA2	cA3	cS1	cS2	i$1	I$2
Rapanea melanophloeos J									*	*					
Rapanea melanophloeos T										*					
Restionaceae sp.1						*	*								
Restionaceae sp.2						*	*								
Restionaceae sp.3							*								
Restionaceae sp.4						*	*								
Restionaceae sp.5							*		*	*					
Restionaceae sp.6							*								
Rhamnaceae sp.1						*									
Searsia angustifolia			*			*									*
Searsia lucida forma *elliptica*												*	*		
Searsia tomentosa												*	*	*	
Rhyncospora brownii									*						
Rubus pinnatus											*				
Rubus sp.1							*		*						
Rubus sp.2															*
Rubus sp.3										*					
Rumex acetosella														*	
Rutaceae sp.1						*									
Salix mucronata S							*	*							
Salix mucronata J				*		*	*	*							
Salix mucronata T				*		*		*							
Selago dolosa														*	
Senecio pterophorus									*					*	
Senecio pubigerus					*						*	*		*	
Senecio rigidus											*	*	*		
Setaria sp.2						*		*							
Solanum nigrum										*	*				
Solanum sp.1								*							
Species 2				*		*	*	*	*	*					
Species 8										*					
Species 9							*	*							
Species 10								*							
Species 11						*									
Species 12						*									
Species 13 S									*						
Species 13 J									*						
Species 13 T									*						
Species 20											*				
Species 21											*				
Species 22															*
Stachys sp.1									*	*					
Stenotaphrum secundatum													*		
Stoebe cinerea									*	*	*				*
Stoebe plumosa			*		*				*			*		*	*

SPECIES	cM1	cM2	cM3	iM4	iW3	cW4	cR5	iR6	cA1	iA2	cA3	cS1	cS2	i$1	l$2
Stoebe sp.1						*	*	*							
Stoebe fusca												*	*		
Struthiola myrsinites									*						
Struthiola sp.1														*	*
Syncarpha vestita													*		
Taraxacum officinale									*	*	*	*	*	*	*
Thymeleaceae sp.1										*					
Thymeleaceae sp.2											*				
Todea barbara	*		*										*		
Tribolium uniolae			*												
Ursinia paleacea									*		*				
Ursinia pinnata											*				
Ursinia sericea					*										
Vellereophyton dealbatum					*			*	*		*				
Virgilia oroboides S										*	*		*		
Virgilia oroboides J									*	*	*		*		
Virgilia oroboides T									*				*		
Wahlenbergia parvifolia														*	*
Wimmerella arabidea					*			*	*						
Wimmerella secunda									*						
Xanthium strumarium				*											
Zantedeschia aethiopica										*	*		*		
Zygophyllum sp.1															*

Table 8.4 Habitat characteristics for species of Fynbos Riparian Vegetation at invaded/cleared rivers (Chapter 6).

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESGINATION	COMMON NAME
Acacia longifolia	Fabaceae	Tree	Riverine, EXOTIC		Long-leaved wattle
Acacia mearnsii	Fabaceae	Tree	EXOTIC		Black wattle
Acacia melanoxylon	Fabaceae	Tree	Riverine, forest, slopes, EXOTIC		Blackwood
Acacia saligna	Fabaceae	Small tree	EXOTIC		Port Jackson
Achyranthes sicula	Amaranthaceae	Forb	Weed		Sicilian achyranthes
Afrocarpus falcatus	Podocarpaceae	Tree	Forest	Facultative	Outeniqua yellowwood
Agathosma crenulata	Rutaceae	Shrub	Slopes and valleys, DRY	Incidental	Buchu
Agrostis lachnantha	Poaceae	Grass	Damp, WET	Obligate	Vinkagrostis
Anthospermum spathulatum	Rubiaceae	Shrub	Clay slopes, DRY	Incidental	
Arctotis revoluta	Asteraceae	Shrub	Rocky slopes, DRY	Incidental	Krulblaargousblom
Aristea capitata	Iridaceae	Forb	Mountain slopes, DRY	Incidental	Blousuurkanol
Aristida junciformis	Poaceae	Grass	Mountain slopes, DRY	Incidental	Wire grass
Askidiosperma chartaceum	Restionaceae	Restio	Marshy mountain slopes, WET	Obligate	
Asparagus africanus	Asparagaceae	Shrub	Moist places, WET	Obligate	Katdoring
Asparagus rubicundus	Asparagaceae	Shrub	Sandy and granite slopes, DRY	Incidental	Katdoring
Asparagus scandens	Asparagaceae	Shrub	Forest	Facultative	Katdoring
Asplenium aethiopicum	Aspleniaceae	Forb	Forest	Facultative	African spleenwort
Asplenium lunulatum	Aspleniaceae	Forb	Forest, WET	Facultative	Spleenwort
Athanasia trifurcata	Asteraceae	Shrub	Flats and rocky slopes, DRY	Incidental	Kouterbos
Berzelia lanuginosa	Bruniaceae	Shrub	Riverine, WET	Obligate	Berzelia
Blechnum attenuatum	Blechnaceae	Forb	Forest	Facultative	Deer fern
Blechnum australe	Blechnaceae	Forb	Forest	Facultative	Southern deer fern
Blechnum capense	Blechnaceae	Forb	Riverine, WET	Obligate	Cape deer fern
Blechnum punctulatum	Blechnaceae	Forb	Forest, slopes, DRY	Incidental	Deer fern
Brabejum stellatifolium	Proteaceae	Tree	Riverine, WET	Obligate	Wild almond
Brachylaena neriifolia	Asteraceae	Small tree	Riverine, WET	Obligate	Bitterblaar
Briza maxima	Poaceae	Grass	Weed		Grootbewertjie

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESGINATION	COMMON NAME
Calopsis paniculata	Restionaceae	Restio	Riverine, WET	Obligate	
Cannamois virgata	Restionaceae	Restio	Riverine, WET	Obligate	
Canthium ciliatum	Rubiaceae	Shrub	Forest	Facultative	Skaapdrolletjie
Canthium inerme	Rubiaceae	Small tree	Forest	Facultative	Cape date
Canthium ventosum	Rubiaceae	Small tree	Forest	Facultative	Klipels
Carpha glomerata	Cyperaceae	Sedge	Riverine, WET	Obligate	Vleibiesie
Carprobrotus edulis	Aizoaceae	Forb	Coastal and inland slopes, DRY	Incidental	Hottentot fig
Cassine peragua	Celastraceae	Small tree	Scrub, forest, woodland	Facultative	Cape saffron
Cassytha ciliolate	Lauraceae	Forb	Various trees and shrubs, DRY	Incidental	False dodder
Chasmanthe aethiopica	Iridaceae	Geophyte	Coastal, bush, forest	Facultative	Cobra lily
Chelianthes contracta	Pteridaceae	Forb	Shady rocks, DRY	Incidental	Lip Fern
Chenopodium ambrosioides	Amaranthaceae	Forb	Weed		Wormseed
Cliffortia atrata	Rosaceae	Shrub	Sandstone slopes, DRY	Incidental	Climber's Friend
Cliffortia complanata	Rosaceae	Small shrub	Moist upper rocky slopes, WET	Obligate	Climber's Friend
Cliffortia cuneata	Rosaceae	Shrub	Lower sandstone slopes, DRY	Incidental	Climber's Friend
Cliffortia dregeana	Rosaceae	Shrub	Sandstone slopes, DRY	Incidental	Climber's Friend
Cliffortia phillipsii	Rosaceae	Shrub	Sandstone slopes, DRY	Incidental	Climber's Friend
Cliffortia polygonifolia	Rosaceae	Shrub	Flats and lower slopes, DRY	Incidental	Paddabos
Cliffortia pterocarpa	Rosaceae	Shrub	Lower mountain slopes, DRY	Incidental	Climber's Friend
Cliffortia ruscifolia	Rosaceae	Shrub	Rocky sandstone soils, DRY	Incidental	Steekbos
Cliffortia subsetacea	Rosaceae	Shrub	Flats and lower mountain slopes, DRY	Incidental	Climber's Friend
Clutia ericoides	Euphorbiaceae	Small shrub	Rocky sandstone slopes, DRY	Incidental	Bliksembos
Conyza bonariensis	Asteraceae	Forbs	Weed		Argentine fleabane
Conyza canadensis	Asteraceae	Forb	Weed		Canadian fleabane
Crassula rupestris	Crassulaceae	Small shrub	Dry stony slopes, DRY	Incidental	Concertina plant
Cryptocarya angustifolia	Lauraceae	Small tree	Riverine, WET	Obligate	Blue laurel
Cullumia ciliaris	Asteraceae	Small shrub	Lower sandstone slopes, DRY	Incidental	Steekhaarbos
Cullumia setosa	Asteraceae	Small shrub	Lower mountain slopes, DRY	Incidental	Steekhaarbos

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESGINATION	COMMON NAME
Cunonia capensis	Cunoniaceae	Tree	Riverine, forest, WET	Obligate	Butterspoon tree
Curtisia dentata	Cornaceae	Small tree	Forest	Facultative	Assegaaibos
Cyperus denudatus	Cyperaceae	Sedge	Riverine, WET	Obligate	Matjiesgoed
Digitaria debilis	Poaceae	Grass	Weed		Finger grass
Digitaria sanguinalis	Poaceae	Grass	Weed		Crab grass
Eckebergia capensis	Meliaceae	Tree	Forest		Cape ash
Ehrharta erecta	Poaceae	Grass	Shady slopes, DRY	Incidental	
Ehrharta ramosa	Poaceae	Grass	Mountain slopes, DRY	Incidental	
Ehrharta ramosa subsp. *aphylla*	Poaceae	Grass	Mountain slopes, DRY	Incidental	
Ehrharta ramosa subsp. *ramosa*	Poaceae	Grass	Mountain slopes, DRY	Incidental	
Ehrharta rehmannii	Poaceae	Grass	Mountain slopes, forest margins, DRY	Incidental	
Ehrharta setacea	Poaceae	Grass	High rocky slopes in damp places, WET	Obligate	
Elegia asperiflora	Restionaceae	Restio	Seeps on sandstone slopes, WET	Obligate	
Elegia capensis	Restionaceae	Restio	Riverine, WET	Obligate	
Elytropappus intricate	Asteraceae	Shrub	Sandstone slopes, DRY		Renosterbos
Epischoenus gracilis	Cyperaceae	Sedge	Mountain slopes, DRY	Incidental	
Eragrostis curvula	Poaceae	Grass	Grassland, DRY	Incidental	Berg soetgras
Eragrostis sarmentosa	Poaceae	Grass	Winter-wet sand, WET	Obligate	Love grass
Erica abietina	Ericaceae	Small shrub	Mountain plateaus, DRY	Incidental	Red heath
Erica bergiana	Ericaceae	Small shrub	Seeps and moist slopes, WET	Obligate	Heather
Erica caffra	Ericaceae	Shrub	Riverine, WET	Obligate	Water heath
Erica canescens	Ericaceae	Small shrub	Coastal flats and lower slopes, DRY	Incidental	Heather
Erica curviflora	Ericaceae	Shrub	Wet or damp areas, WET	Obligate	water heath
Erica curvirostris	Ericaceae	Small shrub	Dry stony areas, DRY	Incidental	Heuningheide
Erica hispidula	Ericaceae	Small shrub	Widespread, DRY	Incidental	Heather
Erica laeta	Ericaceae	Small shrub	Coastal flats of lower slopes, DRY	Incidental	Heather
Erica nudiflora	Ericaceae	Small shrub	Coastal flats, DRY	Incidental	Heather
Erica pinea	Ericaceae	Small shrub	Rocky slopes and plateaus, DRY	Incidental	Heather

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESGINATION	COMMON NAME
Erica sphaeroidea	Ericaceae	?	?		Heather
Erica tenuis	Ericaceae	Small shrub	Rocky wet ledges to open slopes, DRY	Incidental	Heather
Eucalyptus leucoxylon	Myrtaceae	Tree	ALIEN		
Euryops abrotanifolius	Asteraceae	Forb	Weed		Geelmagriet
Ficinia acuminata	Cyperaceae	Sedge	Riverine, WET	Obligate	
Ficinia capillifolia	Cyperaceae	Sedge	Slopes, DRY	Incidental	
Ficinia capitella	Cyperaceae	Sedge	Flats and slopes, DRY	Incidental	
Ficinia indica	Cyperaceae	Sedge	Flats and lower slopes, DRY	Incidental	
Ficinia nigrescens	Cyperaceae	Sedge	Flats, slopes, DRY	Incidental	
Ficinia oligantha	Cyperaceae	Sedge	Lower slopes, DRY	Incidental	
Ficinia tenuifolia	Cyperaceae	Sedge	Lower slopes, DRY	Incidental	
Ficinia trichoides	Cyperaceae	Sedge	Rocky lower to middle slopes, DRY	Incidental	
Freylinia lanceolata	Scrophulariaceae	Small tree	Riverine, WET	Obligate	Heuningklokkiebos
Fuirena hirsuta	Cyperaceae	Sedge	Riverine, WET	Obligate	
Gastridium phleoides	Poaceae	Grass	Weed		
Grammatotheca bergiana	Campanulaceae	Forb	Marshy flats, WET	Obligate	Water lobelia
Hackea sericea	Proteaceae	Small tree	Sandstone slopes, DRY	Incidental	Silky hakea
Halleria elliptica	Scrophulariaceae	Shrub	Riverine slopes, WET	Obligate	Fuschia
Halleria lucida	Scrophulariaceae	Small tree	Coastal bush, forest	Facultative	Tree fuschia
Hartogiella schinoides	Celastraceae	Small tree	Fynbos, forest, woodland, DRY	Incidental	Saffron
Heeria argentea	Anacardiaceae	Tree	Rocky forest and bush, DRY	Incidental	Kliphout
Helichrysum cymosum	Asteraceae	Shrub	Sandy slopes in damp places, WET	Obligate	Strooiblom
Helichrysum odoratissimum	Asteraceae	Small shrub	Sandy slopes in damp places, DRY	Incidental	Strooiblom
Helichrysum patulum	Asteraceae	Shrub	Sandy flats and slopes, often coastal, DRY	Incidental	Strooiblom
Hippia frutescens	Asteraceae	Small shrub	Riverine, WET	Obligate	Rankals
Histiopteris incisa	Dennstaedtiaceae	Forb	Riverine, WET	Obligate	
Homalanthus populifolius	Euphorbiaceae	Small tree	ALIEN		
Hydrocotyle verticillata	Apiaceae	Forb	Riverine, WET	Obligate	Pennywort

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESGINATION	COMMON NAME
Hyparrhenia hirta	Poaceae	Grass	Disturbed areas and grassland, DRY	Incidental	Thatch grass
Ilex mitis	Aquifoliaceae	Tree	Riverine Forest, WET	Obligate	African holly
Indigofera filifolia	Fabaceae	Shrub	Riverine and fynbos, WET	Obligate	Indigo
Inula graveolens	Asteraceae	Small shrub	Weed		Khakiweed
Ischyrolepis cincinnata	Restionaceae	Restio	?		
Ischyrolepis fraternal	Restionaceae	Restio	?		
Ischyrolepis gaudichaudianus	Restionaceae	Restio	Dry rocky slopes, DRY	Incidental	
Ischyrolepis gossypina	Restionaceae	Restio	Light seeps and moist slopes, WET	Obligate	
Ischyrolepis macer	Restionaceae	Restio	?		
Ischyrolepis sieberi	Restionaceae	Restio	Rocky slopes and flats, DRY	Incidental	
Ischyrolepis subverticulata	Restionaceae	Restio	Riverine, WET	Obligate	
Ischyrolepis tenuissima	Restionaceae	Restio	?		
Isolepis digitata	Cyperaceae	Sedge	Riverine, WET	Obligate	
Isolepis ludwigii	Cyperaceae	Sedge	Riverine, WET	Obligate	
Isolepis prolifera	Cyperaceae	Sedge	Riverine, WET	Obligate	
Juncus capensis	Juncaceae	Rush	Damp, slopes, WET/DRY	Facultative	
Juncus effusus	Juncaceae	Rush	Riverine, WET	Obligate	
Juncus exsertus	Juncaceae	Rush	Riverine, WET	Obligate	Biesie
Juncus lomatophyllus	Juncaceae	Rush	Riverine, WET	Obligate	
Kiggelaria africana	Kiggelariaceae	Tree	Forest, DRY	Incidental	Wild Peach
Lagurus ovatus	Poaceae	Grass	Disturbed areas, DRY	Incidental	Haasstert
Laurembergia repens	Haloragaceae	Forb	Boggy, WET	Obligate	
Leucadendron salicifolium	Proteaceae	Shrub	Riverine, WET	Obligate	Cone bush
Lobelia erinus	Campanulaceae	Forb	Slopes, DRY	Incidental	Lobelia
Nemesia affinis	Scrophulariaceae	Forb	Sandy and granite slopes/flats, DRY	Incidental	Cape snapdragon
Nemesia diffusa	Scrophulariaceae	Forb	Sandstone slopes, DRY	Incidental	Cape snapdragon
Nivenia corymbosa	Iridaceae	Shrub	Riverine, WET	Obligate	Bush iris
Oftia africana	Scrophulariaceae	Small Shrub	Rocky sandstone/granite slopes, DRY	Incidental	Lazy bush

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESGINATION	COMMON NAME
Olea capensis	Oleaceae	Small tree	Scrub, forest	Facultative	Ysterhout
Olea europea	Oleaceae	Tree	Forests and rocky slopes, DRY	Incidental	Wild olive
Oncinema lineare	Apocynaceae	Forb	Riverine, WET	Obligate	
Oscularia ornata	Aizoaceae	Small shrub	Rock crevices, DRY	Incidental	Sandsteenvygie
Osmitopsis asteriscoides	Asteraceae	Shrub	Marshes and seeps on sandstone, WET	Obligate	Belskruie
Osteospermum ciliatum	Asteraceae	Small shrub	Sandstone slopes, DRY	Incidental	Bietou
Osteospermum hispidum	Asteraceae	Small shrub	Rocky lower slopes, DRY	Incidental	Bietou
Othonna parviflora	Asteraceae	Shrub	Sandstone slopes, DRY	Incidental	Bobbejaankool
Othonna quinquidentata	Asteraceae	Shrub	Rocky sandstone slopes, DRY	Incidental	Bobbejaankool
Oxalis pardalis	Oxalidaceae	Geophyte	Heavier soils, DRY	Incidental	Sorrel
Panicum schinzii	Poaceae	Grass	Moist sites, WET	Obligate	Blousaadgras
Paraserianthes lophantha	Fabaceae	Small tree	ALIEN		Stinkbean
Paspalum dilatatum	Poaceae	Grass	Weed		Dallis grass
Paspalum urvillei	Poaceae	Grass	Riverine, WET	Obligate	Dallis grass
Passerina vulgaris	Thymelaeaceae	Shrub	Sandy, disturbed flats and slopes, DRY	Incidental	Ganna bush
Pelargonium capitatum	Geraniaceae	Small shrub	Coastal dunes and flats, DRY	Incidental	Kusmalva
Pelargonium cucullatum	Geraniaceae	Shrub	Sandy and granite slopes along coast, DRY	Incidental	Wildemalva
Pelargonium grossularioides	Geraniaceae	Forb	Damp places, WET	Obligate	Malva
Pelargonium scabrum	Geraniaceae	Shrub	Rocky sandstone slopes, DRY	Incidental	Hoenderbos
Pelargonium tabulare	Geraniaceae	Small shrub	Cool slopes, DRY	Incidental	Malva
Pellaea pteroides	Pteridaceae	Forb	Forest, fynbos	Facultative	Myrtle fern
Pennisetum clandestinum	Poaceae	Grass	Clay and loamy soils, DRY	Incidental	Kikuyu grass
Pennisetum macrourum	Poaceae	Grass	Marshes, WET	Obligate	Bedding grass
Pentameris distichophylla	Poaceae	Grass	Rocky sandstone slopes, DRY	Incidental	
Pentameris thuarii	Poaceae	Grass	Lower sandstone slopes, DRY	Incidental	
Pentaschistis airoides	Poaceae	Grass	Light shade on lower slopes, DRY	Incidental	
Pentaschistis aurea	Poaceae	Grass	Cool damp rock ledges, DRY	Incidental	
Pentaschistis barbata	Poaceae	Grass	Coastal sands, DRY	Incidental	

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESGINATION	COMMON NAME
Pentaschistis curvifolia	Poaceae	Grass	Sandstones slopes, DRY	Incidental	
Pentaschistis densifolia	Poaceae	Grass	Sandstone ledges and rock cracks, DRY	Incidental	
Pentaschistis pallida	Poaceae	Grass	Slopes and flats, DRY	Incidental	
Persicaria lapathifolia	Polygonaceae	Forb	Weed		
Persicaria serrulata	Polygonaceae	Forb	Weed		
Peucedanum galbanum	Apiaceae	Small tree	Rocky slopes, forest, bush, DRY	Incidental	Blister bush
Phylica imberbis	Rhamnaceae	Shrub	Sandstone slopes and flats, DRY	Incidental	Hardebos
Phylica oleaefolia	Rhamnaceae	Shrub	Rocky slopes, DRY	Incidental	Blinkhardebos
Phytolacca americana	Phytolacaceae	Forb	Weed		Pokeweed
Phytolacca octandra	Phytolacaceae	Forb	Weed		Inkweed
Pinus pinaster	Pinaceae	Tree	EXOTIC		Cluster pine
Pinus radiata	Pinaceae	Tree	EXOTIC		
Platycaulos callistachyus	Restionaceae	Restio	DRY	Incidental	
Platycaulos subcompressus	Restionaceae	Restio	?		
Platycaulus compressus	Restionaceae	Restio	?		
Platycaulus major	Restionaceae	Restio	?		
Platylophus trifoliatus	Cunoniaceae	Tree	Riverine, WET	Obligate	Witels
Plecostachys polifolia	Asteraceae	Small shrub	Riverine, WET	Obligate	Vaaltee
Pleopeltis macrocarpa	Polypodiaceae	Forb	Forest	Facultative	Shield sorus polypody
Podocarpus elongatus	Podocarpaceae	Tree	Riverine, WET	Obligate	Breeriviervalleigeelhout
Populus X canescens	Salicaceae	Tree	EXOTIC		Grey poplar
Prionium serratum	Prioniaceae	Shrub	Riverine, WET	Obligate	Palmiet
Protea laurifolia	Proteaceae	Tree	Sandstone slopes, DRY	Incidental	Protea
Pseudobaeckia africana	Bruniaceae	Shrub	Riverine, WET	Obligate	
Pseudognaphalium luteo-album	Asteraceae	Forb	Weed		
Pseudognaphalium undulatum	Asteraceae	Forb	Damp grassy or rocky slopes, WET	Obligate	
Pseudopentameris thuarii	Poaceae	Grass	?		
Pseudoselago recurvifolia	Scrophulariaceae	Forb	Stony slopes, DRY	Incidental	Powder puff

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESGINATION	COMMON NAME
Pseudoselago subglabra	Scrophulariaceae	Forb	Sandy slopes, DRY	Incidental	Powder puff
Pseudoselago verbenacea	Scrophulariaceae	Forb	Riverine, WET	Obligate	Powder puff
Psoralea pinnata	Fabaceae	Tree	Riverine, forest, fynbos	Facultative	Fonteinbos
Pteridium aquilinum	Dennstaedtiaceae	Forb	Fynbos, forest	Facultative	Bracken fern
Pycreus polystachyos	Cyperaceae	Sedge	Damp, WET	Obligate	
Quercus robur	Fagaceae	Tree	ALIEN		English oak
Rapanea melanophloeos	Myrsinaceae	Tree	Forest	Facultative	Cape beech
Restio multiflorus	Restionaceae	Restio	?		
Restio perplexus	Restionaceae	Restio	?		
Restio quadratus	Restionaceae	Restio	Slopes, DRY	Incidental	
Searsia angustifolia	Anacardiaceae	Small tree	Riverine, WET	Obligate	Wilgerkorentebos
Searsia crenata	Anacardiaceae	Small tree	Sandy coastal flats. DRY	Incidental	Duinekraaibessie
Searsia lucida	Anacardiaceae	Small tree	Sandy flats and slopes, DRY	Incidental	Blinktaaibos
Searsia tomentosa	Anacardiaceae	Small tree	Rocky slopes, DRY	Incidental	Korentebos
Rhyncospora brownii	Cyperaceae	Sedge	Seeps, WET	Obligate	
Rubus pinnatus	Rosaceae	Shrub	Forest	Facultative	Bramble
Rumex acetosella	Polygonaceae	Forb	Weed		Sheep sorrel
Salix mucronata	Salicaceae	Small tree	Riverine, WET	Obligate	Cape willow
Schizaea tenella	Schizaeaceae	Forb	Riverine, WET	Obligate	Toothbrush fern
Scolopia mundii	Flacourtiaceae	Tree	Forest	Facultative	Rooipeer
Secamone alpinii	Apocynaceae	Forb	Forest	Facultative	
Selago dolosa	Scrophulariaceae	Shrub	Stony and gravelly slopes, DRY	Incidental	Bitter bush
Senecio pterophorus	Asteraceae	Forb	Weed		Ragwort
Senecio pubigerus	Asteraceae	Shrub	Dry stony clay, or granite, DRY	Incidental	Skraalbossie
Senecio rigidus	Asteraceae	Shrub	Sandstone slopes and gullies, DRY	Incidental	Rough ragwort
Solanum nigrum	Solanaceae	Forb	Weed		Nastergal
Stenotaphrum secundatum	Poaceae	Grass	Sandy coastal flats and slopes, DRY	Incidental	Buffelgras
Stoebe cinerea	Asteraceae	Shrub	Rocky slopes, DRY	Incidental	Vaal hartebeeskaroo

SPECIES	FAMILY	GROWTH FORM	HABITAT	DESGINATION	COMMON NAME
Stoebe fusca	Asteraceae	Small shrub	Sandstone slopes, DRY	Incidental	Hartebeeskaroo
Stoebe plumosa	Asteraceae	Shrub	Rocky flat and slopes, DRY	Incidental	Slangbos
Stoebe spiralis	Asteraceae	Small shrub	Damp sandstone slopes, DRY	Incidental	Hartebeeskaroo
Struthiola myrsinites	Thymelaeaceae	Shrub	Sandy soils, DRY	Incidental	Featherhead
Syncarpha vestita	Asteraceae	Small shrub	Rocky slopes and flats, DRY	Incidental	Cape snow
Taraxacum officinale	Asteraceae	Forb	Weed		
Tetraria flexuosa	Cyperaceae	Sedge	Flats to middle slopes, DRY	Incidental	
Thamnochortus lucens	Restionaceae	Restio	?		
Todea barbara	Osmundaceae	Forb	Riverine, WET	Obligate	
Tribolium uniolae	Poaceae	Grass	Clay and granite flats, DRY	Incidental	Koringgras
Ursinia abrotanifolia	Asteraceae	Shrub	Sandstone slopes in damp places, DRY	Incidental	Fynkruie
Ursinia paleacea	Asteraceae	Shrub	Sandstone slopes, DRY	Incidental	Geelmargriet
Ursinia pinnata	Asteraceae	Shrub	Riverine, WET	Obligate	Bergmargriet
Ursinia sericea	Asteraceae	Shrub	Sandstone slopes, DRY	Incidental	Bergmargriet
Vellereophyton dealbatum	Asteraceae	Forb	Damp sandstone, WET	Obligate	
Virgilia oroboides	Fabaceae	Tree	Forest	Facultative	Keurboom
Wahlenbergia parvifolia	Campanulaceae	Small shrub	Riverine, WET	Obligate	African blue-bell
Wahlenbergia rubiodes	Campanulaceae	Small shrub	High rocky slopes, DRY	Incidental	African blue-bell
Wildenowia glomerata	Restionaceae	Restio	?		
Wildenowia incurvata	Restionaceae	Restio	Sandy coastal flats, DRY	Incidental	
Wimmerella arabidea	Campanulaceae	Forb	Water, WET	Obligate	
Wimmerella secunda	Campanulaceae	Forb	Riverine, WET	Obligate	
Xanthium strumarium	Asteraceae	Forb	Weed		
Zantedeschia aethiopica	Araceae	Geophyte	Damp, WET	Obligate	Calla lily

Table 8.5 **Average cover abundance (%) of flowers, fruits and seeds on *S. mucronata* trees at M-up, M-do, S-up and S-do. See Chapter 4. Site codes as per Table 5.1.**

Site	Phenophase	n	2011				2012					
			Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
M-up	Flowers	15	12.3	42.3								
	Fruits	15			35.7							
	Seeds	15				3.3	0.7		1.3			
M-do	Flowers	15	17.1	2.0								
	Fruits	9		15.0	6.0							
	Seeds	7				1.3	6.3					
S-up	Flowers	9	5.3									
	Fruits											
	Seeds											
S-do	Flowers	9	2.3	1.9								
	Fruits											
	Seeds											

Table 8.6 **Average cover abundance (%) of flowers, fruits and seeds on *M. angustifolia* trees at M-up, M-do, S-up and S-do. See Chapter 4. Site codes as per Table 5.1.**

Site	Phenophase	n	2011				2012					
			Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
M-up	Flowers	15				11.0	21.3	8.0	14.7			
	Fruits	15								10.0	11.7	
	Seeds	15	7.7	1.0				7.3				19.7
M-do	Flowers	15			4.3	21.7	17.3	5.3	5.3			
	Fruits	10								8.2	1.8	
	Seeds	10						0.1				5.0
S-up	Flowers	11				4.1	6.4	5.0	6.8	1.4		
	Fruits	12	1.3						0.4	6.5	8.8	
	Seeds	14	8.8	0.3						2.3	7.3	8.0
S-do	Flowers	11				3.3	7.3	4.3	2.3	0.3		
	Fruits	1									0.3	
	Seeds	3	0.6	0.3						0.3	0.3	1.3

Table 8.7 **Average cover abundance (%) of flowers, fruits and seeds on *B. stellatifolium* trees at M-up, M-do, S-up and S-do. See Chapter 4. Site codes as per Table 5.1.**

Site	Phenophase	n	2011				2012					
			Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
M-up	Flowers	13		0.1	1.3	0.7	0.7					
	Fruits											
	Seeds											
M-do	Flowers	4	1.3	5.0	3.7	4.7	2.7	0.3	0.7			
	Fruits											
	Seeds											
S-up	Flowers	15			12.7	9.3	1.7		3.0			
	Fruits	3					1.3	0.7	0.6			
	Seeds	3								0.3	0.3	
S-do	Flowers	6		2.9	3.0	3.3	0.7		0.3			
	Fruits											
	Seeds											